

PHYSIOLOGICAL ASPECTS OF MAIZE (Zea mays L.) YIELD

By

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Abstract of Dissertation Presented to the Graduate Council
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Two experiments were conducted to study physiological reasons for yield differences among diverse maize (Zea mays L.) cultivars. Growth analysis techniques were used to test the hypothesis that high yields of commercial maize hybrids are due to: (1) high rates of dry matter accumulation, (2) a proportionally larger distribution of assimilates to reproductive growth, and/or (3) longer filling period. Attention was also given to storage of assimilates.

In 1978 the single-cross hybrid Pioneer Brand '3369A' was compared with the inbred line Iowa B37, and in 1979 the hybrid 'Coker 77' was compared with two ancient Mexican races, 'Chapalote' and 'Nal-Tel', and a Cuban accession, 'Maiz Criollo'. These experiments were planted at the University of Florida Agronomy Farm in Gainesville at population densities expected to give approximately equal leaf area indices (LAI). Refractometric readings per internode and per unit area were determined in both experiments. Also, in 1979 total available carbohydrate (TAC)

in plant components (stalk, leaf, cob, and grain) were measured. Rates of dry matter accumulation (crop growth rates), computed during the vegetative (CGRv) and reproductive (CGRr) phases, were examined as estimates of canopy capacity to produce assimilates. Ear growth rates (EGR) were also determined. The partitioning coefficient (PC) was used as an estimate of assimilate distributed to ear growth as opposed to vegetative growth, and effective ear filling period (EEFP) and effective seed filling period (ESFP) were estimates of filling periods.

In 1978, the hybrid and inbred ear yields were drastically reduced by poor environmental conditions; however, the hybrid yield was significantly greater than that of the inbred. Stalk refractometric readings per unit land area were higher in the inbred than in the hybrid. This suggested a higher accumulation of soluble solids in the inbred line, probably because of its lower sink capacity.

Except for Nal-Tel, the cultivars compared in 1979 did not significantly differ in CGRv and LAI. However, Coker 77 maintained its high LAI for a longer period than the other cultivars. During reproductive growth, all cultivars showed a decrease in canopy assimilate production. Although CGRr values of Chapalote and Coker 77 were not significantly different, the CGRr of Coker 77 was sustained for a longer period. Maiz Criollo and Nal-Tel had the lowest CGRr values. Partitioning coefficient varied among cultivars. Nal-Tel had the highest PC followed by Coker 77, Maiz Criollo, and Chapalote. Final ear yields for Coker 77, Maiz Criollo, Nal-Tel and Chapalote were 1023, 776, 607, and 578 g m⁻², respectively. Total available carbohydrates were higher in the plant components of Coker 77 than in the other cultivars. Contributions of remobilized TAC from vegetative components to final ear

yield were estimated to be 9, 13, 21, and 26% in Coker 77, Maiz Criollo, Nal-Tel, and Chapalote, respectively.

Similar CGRv values in Chapalote, Coker 77, and Maiz Criollo indicated similar potential to produce high yields. Chapalote, however, produced many barren tillers in addition to ear-bearing stalks. This tillering habit of Chapalote explains its lower PC and yield. Nal-Tel had the highest PC, but its ear yield was low probably because of its low LAI. Length of filling period, either as EEFP or ESFP, was not a significant factor in yield differences. Coker 77 had the highest EGR; differences in EGR accounted for most of the yield differences among cultivars.

The results of these experiments suggested that under conditions of similar LAI, the physiological characteristics of a high-yielding maize cultivar are high PC, high EGR, and a longer duration of CGRr.

INTRODUCTION

While it is generally recognized that commercial hybrid maize (Zea mays L.) cultivars outyield their inbred parents, or ancient races (Duncan and Hesketh, 1968), the physiological and ecological bases for their increased yield have not yet been adequately explained.

A basic step toward increasing the yield of any crop is to understand its pattern of dry matter accumulation. When only final economic yields are determined, little knowledge can be gained on how high yields are achieved. However, growth analysis is an effective way to study the dynamics of dry matter accumulation and yield physiology.

The experiments discussed in the following pages permitted observation and recording of physiological responses of hybrid maize when compared with an inbred line, and with ancient races of Central and North America. However, the main objective was to investigate which of three major hypotheses for differences in yield among cultivars best explained the higher yield of hybrid maize. These hypotheses are:

- i) Higher yielding cultivars have higher crop canopy photosynthetic efficiency. Cultivars with more efficient canopy photosynthesis would produce more assimilates with a given amount of solar radiation and should produce higher yields. The crop growth rate (CGRv) after the canopy has reached 97% ground cover (light interception) and prior to ear development, reflects canopy assimilate production which can go to grain fill.
- ii) High yielding cultivars have longer duration of the effective grain filling period. The longer the grain filling period a

cultivar has the more solar radiation it can intercept to produce photosynthate for ear growth. iii) High yielding cultivars have different distribution of assimilates between reproductive and vegetative growth during the period of ear establishment. A cultivar with greater distribution of assimilates to the reproductive sink during the grain setting period should have greater yield.

It was hoped that this study would help elucidate differences in yield among hybrid, inbred, and ancient races in terms of physiological parameters.

LITERATURE REVIEW

Increase in dry weight is a useful definition of growth for scientists interested in crop productivity. Crop growth is usually more accurately characterized by measurement of dry weight than measurements of fresh weight, which can be strongly influenced by prevailing moisture conditions. However, dry weight increase is not a completely satisfactory definition of growth; because growth also includes germination during which dry weight is lost, cell multiplication and increase in volume both may represent little change in dry weight (Salisbury and Ross, 1969).

Dry weight increase has been described mathematically as a function of physiological, phenological, and environmental factors. Increase in dry weight with time is usually characterized by a sigmoidal curve (Leopold and Kriedemann, 1975), in which three primary phases are recognized: expansion, linear, and senescence (Richards, 1969). In the expansion phase, the growth rate (increase in dry weight per unit of time) is initially slow but the rate increases continuously as more dry weight is added. Growth of a higher plant during its exponential phase is analogous to the accumulation of capital at a continuous compound interest and can be described by the equation $W_t = W_0 (1 + r)^t$, where W_0 is the initial weight, r is the rate of growth or capacity to add dry weight (Blackman, 1919), and W_t is the total dry weight after a certain time t . Accumulation of dry weight is exponential until self-shading or other conditions prevent the increasing leaf area from

producing a proportionate increase in the weight of the plant (Watson, 1958; Leopold and Kriedemann, 1975; Duncan et al., 1967).

The end of the expansion phase marks the beginning of the linear phase in which the increase in dry matter continues at a constant rate. The final, senescence phase is characterized by a decrease in growth rate as the crop approaches maturity and begins to senesce (Salisbury and Ross, 1978).

Growth analysis, by periodic harvest, is a useful tool to characterize and describe these growth phases of single plants or plant communities (McKinion et al., 1974). The use of relative growth rate (RGR, $\text{g g}^{-1} \text{ time}$), net assimilation rate (NAR, $\text{g dm}^{-2} \text{ time}^{-1}$), and leaf area ratio (LAR, $\text{dm}^2 \text{ g}^{-1}$) to quantitatively analyze plant growth has become known as "growth analysis." The measurement of the total dry weight of plant material per unit land area and the measurement of the assimilatory system are the two parameters needed to conduct a growth analysis of a plant community (Radford, 1967). The assimilatory system of a plant community is generally computed as the total leaf area (one side) per unit land area and is known as the leaf area index (LAI) of a canopy (Watson, 1947a and 1947b).

The introduction of the crop growth rate (CGR) function (Watson, 1958), to the traditional "growth analysis," has been recognized (Williams et al., 1965b) as the most meaningful growth function, since it represents the net results of photosynthesis, respiration, and canopy area interactions. As noted by Williams et al., CGR is also representative of the most common agronomic measurement, i.e., yield of dry matter per unit of land area.

The CGR is defined as the increase in plant material per unit land area per unit time. The mean CGR over a time period t_1 to t_2 is given by $CGR = (W_2 - W_1) / (t_2 - t_1)$, where W_1 and W_2 designate the total dry weights at periods t_1 and t_2 , respectively (Watson, 1958). Thus, CGR represents total dry matter productivity of a plant community and, except for a small mineral component, it can be equated as an estimation of net carbon fixed for a crop canopy (Duncan et al., 1978).

Crop growth rate shows a close relationship to LAI in all plant communities, especially below LAI of four (Duncan, 1975). For certain crops such as kale (Brassica oleracea L.), subterranean clover (Trifolium subterraneum L.), sunflower (Helianthus annuus L.), and rice (Oryza sativa L.) optimum LAI values have been shown to exist (Watson, 1958; Black, 1963; Takeda, 1961; Hiroi and Monsi, 1966; Yoshida, 1972). According to these authors increasing LAI beyond the optimum caused a decline in CGR, which was attributed to mutual shading of leaves, such that further increase in leaf area did not compensate for the reduction in net photosynthesis because of less effective illumination. The community still gained dry weight at high LAI, but the rate diminished (Leopold and Kriedemann, 1975). However, experiments with mixed pastures by Brougham (1956), sugar beet (Beta vulgaris L.) by Watson (1958), maize (Zea mays L.) by Williams et al. (1965b), soybeans (Glycine max L., Merr.) by Shibbes and Weber (1966), and rape (Brassica napus L.) by Clarke and Simpson (1978) have not displayed an optimum LAI. The CGR response to LAI for corn does not indicate a peak in CGR at some optimum LAI (Williams et al., 1965b; Duncan, 1975); rather, the trend of the curve, after the initial rise at the low end of the LAI range, is toward an asymptotic plateau. Decline in CGR at later stages

of the growth cycle of corn has been associated partly to the decline in radiation received as the season advances (Duncan et al., 1967; Williams et al., 1968). The asymptotic relationship between CGR and LAI has also been demonstrated for wheat (Triticum aestivum L. em Thell.) by Puckridge and Donald (1967), soybean by Shibles and Weber (1965), and rape by Clarke and Simpson (1978). One explanation for the plateau at high LAI values has been elucidated by experiments in cotton (Gossypium hirsutum L.) by Ludwig et al. (1965), and white clover (Trifolium repens L.) by McCree and Troughton (1966a, 1966b). These authors demonstrated that respiration in shade-adapted leaves of the basal strata in dense canopies of these crops is lower than in leaves exposed to more intense illumination. Thus, CGR may attain a plateau rather than decline beyond an optimal value of LAI. Watson (1958) stated and Williams et al. (1965a, 1965b, 1968) confirmed that the form of the curve relating CGR to LAI and the maximum value of CGR are determined by the way in which the spatial distribution of leaves effects the utilization of incident radiation. Furthermore, at high LAI vertical leaves allow more uniform light incidence, enhancing CGR (Williams et al., 1968). This depends upon light intensity (Kriedemann and Smart, 1971) and adaptation in respiration rates, since lower leaves are not parasitic as was once thought (Ludwig et al., 1965; McCree and Troughton, 1966a, 1966b).

Computer simulations by Duncan (1971) suggested that leaf angle in maize has small effects on photosynthetic rates of a crop canopy per unit land area at LAI values lower than four. Williams et al. (1965a, 1965b, 1968) have shown, however, that the difference in light interception in the range of LAI of 2.7 to 4.5 can be as high as 30%

and that CGR varied proportionally. Their research was conducted with a single-cross hybrid, Dekalb Brand 805, over a wide range of population densities varying from 1.15 to 12.5 plants per m^2 . These experiments point to the conclusion that the amount of irradiance intercepted by the canopy is a major determinant of the CGR during the vegetative phase of maize growth where nutrients and soil moisture are not limiting.

Grain yield correlates well with CGR up to an optimum density. Decline in yield at high populations is mainly due to barren plants (Prine, 1971; Yoshida, 1972; Duncan, 1975). However, an increase in grain yield with increase in planting rate normally ceases before significant number of barren stalks are found. This yield plateau occurs when light interception by the canopy is essentially complete so that little increase in photosynthesis per unit land area is possible (Prine, 1971; Duncan, 1975).

The grain yield of a crop is the product of the average rate of grain dry matter accumulation per unit area and the effective duration of grain filling. The effective period of grain filling (EFP) is defined as the quotient of final reproductive dry weight and the average rate of grain dry matter accumulation per unit area (Daynard et al., 1971). The average reproductive dry-weight accumulation rate can be estimated from the slope of a plot of reproductive dry weight against time during the linear phase (Johnson and Tanner, 1972b; Duncan, 1973).

An alternative method of measuring relative differences in the duration of the grain filling period involves the use of black-layer development and silking date. Black-layer at the base of the nucellus of maize kernels coincides with maximum kernel dry weight (physiological maturity) and marks the end of the filling period (Daynard and Duncan,

1969; Daynard et al., 1971; Daynard, 1972). Thus, total filling period can be estimated on a phenological basis as days from pollination to black-layer formation.

A linear relationship has been found among corn cultivars between grain yield and duration of the phenologically estimated total filling period (Funnah, 1971), and between grain yield and duration of the EFP (Daynard et al., 1971; Daynard, 1972). In Daynard's experiments, yield was more highly correlated with EFP than with the rate of filling. In a comparison between inbreds and hybrids, Johnson and Tanner (1972a, 1972b) found the EFP to be much longer in the hybrids, but their rates of growth per unit area were also higher. Several authors (Daynard et al., 1971; Peaslee et al., 1971; Egli and Leggett, 1976) have suggested that an extension of the filling period will result in higher yields, provided that the rate of dry matter accumulation does not change, the grain has larger potential size, and environmental and nutritional conditions do not limit yield.

Estimation of maize grain yield as the product of mean ear growth rate multiplied by EFP is convenient, since it evades the assessment of the lag phases either at the beginning or at the end of ear growth (Duncan, 1975). The initial lag period, from pollination to the beginning of EFP, may be important in relation to the number of kernels in each inflorescence. Among wheat cultivars, the longer the initial lag phase the more kernels there were in each ear (Rawson and Evans, 1971), especially at low temperatures (Sofield et al., 1974). However, the length of the lag phase in wheat is only a few days, whereas in maize it is between 15 to 18 days (Evans, 1975), comprising from 47 to 84% as long as the effective duration of grain filling (Johnson and

Tanner, 1972a, 1972b). This much longer duration of the lag period may be associated with the presence of 10 to 100 times as many grains per inflorescence in maize compared with wheat, and may be necessary to allow the later florets in the maize inflorescence to set grains (Evans and Wardlaw, 1976).

Recently, investigations have been reported that give insight into which of the parameters, rate or duration, can be most easily modified to increase the final yield. Gay et al. (1980) investigated the physiological basis for the difference in yield between old, low-yielding, and new, high-yielding soybean cultivars in two maturity groups. They concluded that the increase in yield between new and old varieties has been the result of increased length of the filling period. However, Duncan et al. (1978), in a similar study with peanut (*Arachis hypogaea* L.), assessed equal importance to duration of the filling period and growth rates.

Daynard and Kannenberg (1976) provided results supporting the suggestion that selection for a longer EFP represents a feasible means of increasing yields of corn; in their experiments, however, differences in filling period accounted for only a limited portion of the total variation in yield among 30 hybrids in one experiment and 35 in another. They also noted that some of the high-yielding hybrids had shorter than average filling periods in both experiments. Contrastingly, some of the hybrids had long filling periods and below average yields. They speculated that length of filling period and yield are set primarily by the size of the ear sink capacity, i.e., kernel number, established soon after flowering, and kernel size, which is to a large extent genetically controlled.

With a given rate of grain dry-matter accumulation, larger kernel weight may allow a longer filling period and higher yield, assuming that supply of assimilates is adequate to satisfy ear demands.

Duncan et al. (1978) proposed the concept of partitioning, defined as the division of daily assimilate between reproductive and vegetative plant components, and concluded that the yield increase in newly developed peanut cultivars has been the result of higher partitioning to reproductive sink. However, the possibility of yield improvement from an increase in the partitioning of the photosynthate to seed would be reduced when partitioning approaches the maximum (Gay et al., 1980). In the study reported by Duncan et al. (1978) the old peanut cultivars partitioned poorly whereas new peanut cultivars were approaching a maximum. In maize, partitioning and daily photosynthate supply determine kernel number set during or shortly after silking. A relatively large kernel set would be beneficial since the sink demand (kernel number times growth per seed) would determine the rate of utilization of assimilate, whether from photosynthesis and/or from labile storage (W. G. Duncan, Professor of Agronomy, University of Florida, personal communication). However, another possibility for establishment of the sink may be by setting the kernel size soon after flowering, as Wilson and Allison (1978a) suggested; perhaps this occurs once the number of endosperm cells has been determined (Wardlaw, 1970). Wilson and Allison (1978b) found that the removal of alternate plants in the field had little effect on the average weight per kernel of the remaining plants when it was done more than two to three weeks after silking, but increased final average kernel weight when removal of plants was done close to

the time of silking. Very similar results have been reported by Prine (1971) who worked with semi-prolific maize hybrids.

The assimilate used for ear growth may come from current photosynthate produced by the canopy or from labile assimilate stored earlier in the vegetative component, particularly in the basal internodes (Duncan, 1975). Normally, the high rate of photosynthate utilization by the growing plant does not permit a substantial accumulation of assimilates (Duncan, 1975; McPherson and Boyer, 1977); however, many studies (Singh and Nair, 1975; Campbell, 1964; Jurgens et al., 1978; Hume and Campbell, 1972) have revealed that previously stored assimilate can be mobilized and utilized for grain filling, even when all leaves were removed and the entire plant was wrapped in foil (Duncan et al., 1965). The results of these experiments have clearly demonstrated that assimilates can be translocated from other plant components to the ears; however, it is also likely that storage of soluble materials occurs when photosynthate exceeds utilization, and depletion when the demand is greater than the amount of assimilates produced by photosynthesis. Incomplete utilization of photosynthate for grain would also occur in cultivars in which the grain matures before leaf senescence (Duncan, 1975). In such cases, an assessment of the soluble materials accumulated in the stem sap could provide useful information about yield-limiting factors. That is, if sink is limiting, soluble materials should accumulate during the period of active ear filling since assimilate production exceeds utilization. On the other hand, if photosynthesis is limiting, soluble materials should decline as utilization exceeds supply. Indeed, the decrease in stalk weight before and shortly after anthesis and its subsequent

decrease during ear filling show the storage and utilization of soluble solids (Hume and Campbell, 1972; Vietor et al., 1977; Major et al., 1972; Johnson and Tanner, 1972a).

Normally, in a maize field, there is considerable variation among plants in Brix readings of stalk-sap. The Brix reading is an expression of the refractometric index using the correspondent percent of dissolved sucrose which would give a similar index. Willaman et al. (1924), in an intensive study of the possibilities of using corn-stalk juice as a source of syrup, found that the stalk-sap of sweet corn at the canning stage had a density of 9 to 10° Brix. After standing 10 to 20 days following removal of the ears, the stalk-sap density was reported to increase up to 13 to 17° Brix, with sucrose in some plants reaching as high as 15%. Clark (1913) and Bodea (1934) have shown that the expressed juice of maize stalks contains from 10 to 12% sugar at the time of ear formation and as high as 17% sugar if pollination is prevented. Duncan (1975) reported that from corn plants selected at random, stalk-sap Brix readings from lower internodes ran from 3 to 11%. He suggested that this variation probably reflected differences in sink capacity and/or inadequate photosynthetic rates, and that stalk Brix readings could furnish diagnostic indications, pointing to causes for yield limitations of varieties and locations. Van Reen and Singleton (1952) showed that reliable comparisons between varieties can be made using Brix readings. However, they also pointed out that caution should be taken, since some varieties could store much of the sugars as hexoses rather than sucrose, or the concentration of salts and non-sugars components may be high. They recommended that in order to apply the hand

refractometer to other varieties with some assurance as to the meaning of the results, sucrose should be determined chemically with at least a few samples over the range of Brix values encountered.

Assimilate remaining in maize stalks at the end of the growing cycle represents energy fixed by photosynthesis that was not converted into grain, and hence a loss of potential yield. A complication is the fact that lodging is negatively correlated with sugar content in the stalks (Mortimer and Ward, 1964; Campbell, 1964). Campbell (1964) studied three single-cross corn hybrids and showed that structural tissues and vascular systems, the insoluble fraction, from unpollinated and pollinated plants did not differ significantly. Unpollinated plants accumulated more total dry matter in stalks and leaves than pollinated plants. The difference in stalk dry matter was readily accounted for as soluble solids. His results showed an inverse relationship between ear dry matter and soluble solids in the sap just before maturation. The prolific, high-yielding, lodging-susceptible hybrid maintained a soluble solids level in the stalk juice between 8 to 10% Brix. Non-prolific, low-yielding, but lodging-resistant hybrids gradually attained concentrations of 12 to 14%. Non-lodging unpollinated plants of all hybrids accumulated soluble solids from 15 to 17% Brix. Campbell concluded that since pollinated and unpollinated plants differed primarily in stalk soluble-solids content, this stalk component influenced final stalk strength and, therefore, lodging resistance. Thus, selection of varieties for resistance to lodging operates against complete utilization of assimilates for grain.

Photosynthesis provides essentially all the increase in crop weight and all of the metabolic energy required for crop development.

The course of photosynthesis is thus a major determinant of crop yield. In maize the leaf blades are the main photosynthetic organs. Allison (1964) found leaf blades to comprise more than 80% of the total green surface at both anthesis and maturity. Crop growth rate depends on both the rate of leaf area expansion and the rate of photosynthesis per unit leaf area. During early growth, the rate of leaf area expansion is of greatest importance; however, once the leaf canopy has closed, canopy photosynthetic rate becomes the most important determinant of CGR depending on climatic conditions and canopy architecture (Duncan, 1971).

A vertical leaf arrangement is usually desirable in dense crops. Maize cultivars generally have a leaf arrangement intermediate between horizontal and vertical (Allison and Thomas, 1974). McCree and Kenner (1974) felt that the degree of change in leaf angle which is likely to be practicable probably would not have a marked effect on crop assimilation. Furthermore, optimum leaf arrangement for various conditions is far from clear because of the possible influence of factors other than the light relations to which attention is usually confined (Evans, 1975). Differences in leaf arrangement are probably of little importance in maize stands with an LAI of 3 to 4 (Loomis and Williams, 1969; Duncan, 1971).

From a survey of 22 races of maize, ranging from ancient varieties to a modern hybrid, Duncan and Hesketh (1968) found no evidence that improvement of maize over the centuries has been associated with increase in leaf photosynthetic rate. There were, however, differences among races in the way their photosynthetic rates responded to temperature, which appeared to be adaptive. High-altitude races, for

example, had relatively lower rates at high temperature, but did not differ from low-altitude races at low temperatures. The ancient races had net photosynthetic rates near the average for all races. In their experiment, only the modern single-cross hybrid ranked consistently high in photosynthetic rates at all temperatures. Differences among maize cultivars in photosynthetic rates have been reported, but rate differences appear to be dependent on environmental conditions. Rate differences found by Heichel and Musgrave (1969) in the Philippines were not always apparent at Cornell University at Ithaca, New York (Gifford, 1970). Similarly, although heterosis in photosynthetic rates was reported by Heichel and Musgrave (1969) and Derieux et al. (1973), there are other studies where it was not found (Duncan and Hesketh, 1968).

Apparent photosynthesis (Shibles, 1976) has been shown to decrease as leaves age. Viator et al. (1977) studying the effect of leaf age on photosynthetic rates in maize showed decreases in apparent photosynthesis of individual leaves at different positions in the stalk. The study was done in greenhouse and field cultured open pollinated varieties, inbred lines, and single-cross hybrids. Mean apparent photosynthetic rates across leaf position at pre-tassel, silking, and dough stages for one inbred line were 52.8, 39.1, and 20.0 mg CO₂ dm⁻² h⁻¹, respectively. These measurements were done under greenhouse conditions. In an open-pollinated, field grown cultivar, mean apparent photosynthetic rate at the same stages as above and across leaf positions were 58.1, 45.0, and 28.7 mg CO₂ dm⁻² h⁻¹. Pre-tassel, silking, and dough stages were at 44, 71, and 88 days after emergence, respectively. Their measurements of apparent photosynthesis in eight

single-cross hybrids at the silking stage ranged from 68.7 to 55.2 $\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$. The silking stage was recorded 71 days after emergence; the measurements were done on the leaf immediately above the ear. At the dent stage, 110 days after emergence, the range was 48.7 to 36.9 $\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$. Leaf area index at the silking stage ranged from 4.31 to 4.12, and at the dent stage from 4.08 to 3.99. Thus, their study showed a reduction in mean apparent photosynthesis of more than 62% in inbred lines, 50% in open pollinated varieties, and 32% in single-cross hybrids from the early stages to the latest one. They attributed the decrease in mean apparent canopy photosynthesis to the decrease in mean leaf photosynthesis as caused by leaf aging.

Crosbie et al. (1977) also have shown a decrease in leaf photosynthetic rate from the vegetative to the reproductive stage. They studied photosynthetic rate variability in 64 inbred lines, which were selected randomly from a set of 247 inbred lines developed from Iowa Stiff Stalk Synthetic (BSSS) population. They showed decreases of 30% in the mean CO_2 exchange rate (Shibles, 1976) from measurements performed at stage 3.5 (twelfth leaf completely visible) to measurements taken at stage 6.0 [12 days after silking or "blister" stage (Hanway, 1971)]. At stage 3.5 they measured 36.6 $\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ from the most recently expanded leaf. At stage 6.0 they measured 25.7 $\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ from the second leaf below the tassel.

Wilhelm and Nelson (1978b) studied leaf growth, leaf aging, and photosynthetic rates in tall fescue (Festuca arundinacea Schreb) genotypes. The genotypes were selected (Wilhelm and Nelson, 1978a) to represent four carbon-exchange rate-yield categories: high CER-high yield, high CER-low yield, low CER-high yield, and low CER-low yield.

Their experiment showed that CER of all four genotypes decreased after collar formation at a rate of about 15 to 20% per week. They grew one crop in the greenhouse during a four week period and another in the field during a six week period. The CER measurements were done in leaves previously marked and the rates were measured at an approximate interval of one week on clear days.

Another possible reason for the decrease in photosynthetic rates can be ascribed to increases in nonstructural carbohydrates (NSC) in the leaves. Decreased photosynthetic rates with a concurrent increase in NSC were observed in soybean following pod removal (Mondal et al., 1978). On the other hand, an increase in photosynthetic rates of leaves during fruit formation has also been observed in soybeans (Dornhoff and Shibles, 1979; Ghorashy et al., 1975). This effect has been hypothesized to be due to an increased demand for photosynthates by the developing fruit with a resulting decrease in NSC. Decreased NSC concentration has been thought to stimulate photosynthesis by alleviating end product inhibition by soluble sugars (Neales and Incoll, 1968), or by decreasing starch concentration of leaves (Nafzinger and Koller, 1976; Thorne and Koller, 1974; Upmeyer and Koller, 1973). High starch levels may inhibit net leaf photosynthesis by starch granules physically shading the chloroplasts, by increasing biochemical carboxylation resistance, or by increasing the CO₂ diffusion pathlength due to physical swelling of chloroplasts (Nafzinger and Koller, 1976).

Hageman et al. (1976) reviewed their attempts to screen and select corn varieties for activity of specific essential enzymes (aldolase, glucose 6-phosphate dehydrogenase, trisephosphate dehydrogenase, and

nitrate reductase). Genetic differences in activities of single enzymes were found among cultivars; however, these did not provide a metabolic explanation for hybrid vigor in dry matter production, because crosses did not exhibit heterotic enzyme activity when compared with the parental inbreds. On the basis of their failure to find single enzyme activities to account for heterosis, they suggested that an efficiently organized total metabolic system is the characteristic of a superior corn variety.

MATERIALS AND METHODS

This study was conducted at the Agronomy Farm of the University of Florida during the 1978 and 1979 growing seasons. The soil used in 1978 was a poorly drained, loamy, silicious, hyperthermic Arenic Paleudult (Kendrick loamy sand). In 1979, the soil was a taxajunct classified as loamy, mixed, thermic Arenic Hapludalf (Jonesville fine sand) with excellent drainage.

Rainfall, solar radiation, and maximum and minimum temperatures, collected near the plots at the Agronomy Farm Weather Station, were averaged over 10-day periods coinciding with harvest dates. These data for 1978 and 1979 are presented in Figs. 1 and 2. Anthesis dates were recorded in both years when 50% of the plants in each plot were shedding pollen. General information on fertilizers and pesticides is presented in Table 1.

In 1978, the experiment was seeded on June 9. The corn cultivars, single-cross hybrid Pioneer Brand 3369A and inbred line Iowa B37, were planted in a complete randomized design with four replications. The seeds were hand planted on square spacing of approximately 45 cm for the hybrid and 30 cm for the inbred. Two or three seeds were placed at each planting point to insure uniform stands. Fifteen days after emergence the plants were thinned to one per planting point. Final plant populations were 4.8 and 10.8 plants per m² for the hybrid and inbred, respectively. Nitrogen was applied 30 days after planting at

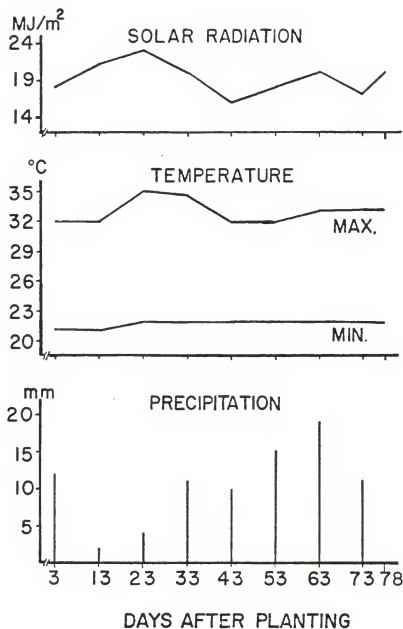


Figure 1. Climatological data for the 1978 experimental period. Averages of 10-day periods coinciding with harvest dates.

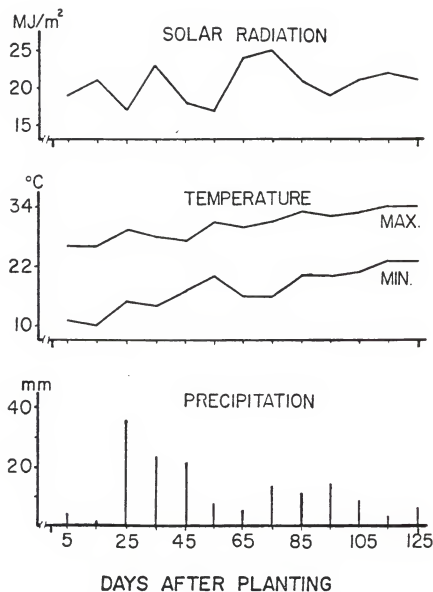


Figure 2. Climatological data for the 1979 experimental period. Averages of 10-day periods coinciding with harvest dates.

Table 1. Fertilizers and pesticides used in the maize growth analysis experiments of 1978 and 1979.

Product	Rate kg/ha	Application Date
<u>1978 Experiment (9 June through 25 August)</u>		
Fertilizers:		
Dolomite	2000.0	1 month before planting
4-8-16	600.0	1 month before planting
Nitrogen	80.0	30 days after planting
Nitrogen	30.0	45 days after planting
Nematicides:		
Carbofuran	1.5 ai	1 week before planting
DBCP	12.0 ai	1 week before planting
Herbicides:		
Butylate	3.0 ai	Pre-emergence
Atrazine	2.0 ai	Pre-emergence
Insecticide:		
Carbaryl	0.5-1.0 l/ha ai	When necessary
<u>1979 Experiment (21 March through 23 July)</u>		
Fertilizers:		
4-8-16	600.0	10 days before planting
Nitrogen	40.0	30 days after planting
Nitrogen	40.0	45 days after planting
Herbicides:		
Butylate	3.0 ai	10 days before planting
Atrazine	2.0 ai	10 days before planting
Nematicides:		
Carbofuran	1.5 ai	At planting
Insecticide:		
Carbaryl	0.5-1.0 l/ha ai	When necessary

different rates because of the different plant populations. The densities used gave similar LAI values for both cultivars throughout the critical part of the experimental period.

Sampling began 23 days after planting and continued at intervals of 10 days until day 73. The last sampling at day 78 had a 5-day interval. Samples were taken from each plot beginning at one end and moving successively across the field, leaving one or two border rows between sampling sites. The plants were removed from the soil with a shovel to insure extraction of most of the root weight. From the third harvest until the last sampling date, the roots were left in the soil on the assumption that minimum additional root growth was taking place (Hanway, 1963, 1971; Whaley et al., 1950).

Total dry matter production of both hybrid and inbred cultivars was calculated for harvests 3 to 6 by adding the root weight of harvest 2 to the other plant components on each respective harvest date. Six harvests were taken, each consisting of three subsamples as follows:

- i. Ten plants per plot were harvested to measure the total fresh weight. Ear fresh weight was determined separately.
- ii. An average plant was selected from each plot and used to determine fresh and dry weight of plant components: roots, stalk (stem and sheaths), leaves, and ears. These plant components were dried at 60° C for three days. Leaf area was measured with a photo-electric planimeter (Hayashi Denko Co., Ltd., Automatic Area Meter, Type AAM-5) and used to calculate LAI. The ratio dry weight to fresh weight of the whole plants, and of the ears, was used to estimate total as well as ear dry weights of the 10-plant sample.

iii. Six plants from each plot were sampled to estimate soluble solid concentrations in the internodes. An American Optical 0 to 25% Brix hand refractometer was used. The Brix readings were measured in the second, fourth, sixth, and eighth internodes, beginning from the base. Brix readings were taken until day 83.

In 1979, four cultivars were studied: Coker 77, a closed-pedigree, high yielding hybrid; Maiz Criollo, a racial accession from Cuba; and Chapalote and Nal-Tel, two ancient Mexican races. Chapalote and Nal-Tel are races believed to have arisen from primitive sources without hybridization (Wellhausen et al., 1952). The experiment was hand-planted on March 21 in a split-plot arrangement with four replications. Ten main plots, each representing a harvest date, were arranged in such a way that two border rows of Coker 77, planted continuously in the middle of the experimental area, separated each replication into two sets of five main plots. Additionally, two border rows of Coker 77, in the outside of the main plots, were planted to insure equal competition among cultivars. The sub-units consisted of two rows per cultivar without border separation between sub-units in the same main plot. Each sub-unit contained 24 planting sites. One or two seeds were placed at each planting site. Twenty plants were used for sampling and two plants, each at the row's ends, were utilized as guard plants between sub-units of the other main plots. Missing sites were replanted with plants of equal age and size, resulting in nearly perfect stands for all cultivars. Final plant population was 4.3 plants per m². Harvest dates and cultivars were randomly assigned to main plots and sub-units, respectively, by means of a table of random numbers. Overhead irrigation

was applied at planting to encourage uniform germination and provide adequate soil moisture during periods of low rainfall.

Sampling began 34 days after emergence. The second sampling was made 11 days later. Subsequent sampling continued at 10-day intervals until 125 days after planting with a total of 10 harvests. Each sample consisted of three sub-samples as follows:

- i. Five plants were selected from each sub-plot and used to estimate the internode density in Brix readings. The readings were made on alternate internodes beginning in the second internode at ground level. Juice from the internode was obtained by squeezing the basal end with pliers. Several drops of juice were placed onto the glass surface of an American Optical 0 and 25% Brix hand refractometer for its reading. Readings were performed only for the main stalk.

These five plants were also used to determine the percent dry matter distribution of vegetative and reproductive plant components. A plant consisted of the main stem plus any tillers. From the ears, a random sample of 100 kernels was weighed to estimate the average kernel weight (AKW). From the plot of AKW and time the rate of kernel dry matter accumulation (KGR) was estimated using linear regression analysis (Steel and Torrie, 1960). Effective seed filling period (ESFP) was calculated by the ratio AKW to KGR.

Stalk (stems and sheaths), leaf blades, cobs, and kernels were ground in a Wiley mill with 1-mm screen. Cobs and kernels were ground again to pass through a 40 mesh screen. Total available carbohydrates (TAC) were determined in the ground material by the procedure outlined in Appendix B. The fractions included in the TAC determination are:

the reducing sugars, glucose and fructose; the transport sugars which are nonreducing, mainly sucrose; and the storage carbohydrates, mainly sucrose and starch.

ii. Ten plants in each sub-unit were harvested and dried in a convection oven at 60°C for four days. The measured total dry weight was added to the total dry weight of the five-plant sample, such that total dry weight of 15 plants was used to calculate the CGR and ear growth rate (EGR) of each cultivar. Dry matter distribution of the 15-plant sample, in grams per m^2 and for each variety, was estimated by multiplying its total dry weight by the percent dry matter calculated from the 5-plant sample.

iii. A representative plant from each sub-unit was sampled for leaf-area determination. Leaf area was measured with a Lambda Instrument Corp., LI-3100 Area Meter, and utilized to estimate LAI.

Total available carbohydrates, in grams per m^2 , were calculated by multiplying each component (stalk, leaves, cobs, and grain) of the 15-plant sample by the percentage TAC in each part.

Crop growth rate and EGR for each cultivar were calculated by simple linear regression analysis applied during the linear phase of the 15-plant sample total and ear dry-matter accumulation curves (Steel and Torrie, 1960).

Effective ear filling period (EEFP) was estimated by the quotient of final yield and EGR. Number of kernels per m^2 was calculated by dividing the product of ear yield times shelling percentage by AKW.

In all rates of dry matter accumulation determinations, separate linear regression equations were computed for each replication. The slopes of these lines were used as treatment variables for statistical

analysis of dry matter accumulation rates. All characteristics observed or calculated were tested by analysis of variance and ranked by Duncan's Multiple Range procedure at the 0.05 level of probability. Statistical analyses were done with the use of SAS 79.3 Statistical Analysis System by Barr et al. (1979). Analysis of variance and regression analysis were performed using the ANOVA (analysis of variance) and the GLM (general linear models) procedures.

RESULTS AND DISCUSSION

1978 Experiment

Vegetative Yields

Late planting in 1978 together with poor soil drainage resulted in unfavorable conditions for a proper development of both the hybrid and inbred cultivars. Prine and Schroder (1965) showed that late planting decreased the growth cycle of the semi-prolific hybrid Florida 200 by more than 30 days from planting to 50% silking. They found that yield for maize planted on May 8 was 40% lower than that planted March 8. In 1978, rainfall during the month of June was adequate for crop growth. However, rainfall in July and August was 30% and 17% higher, respectively, than the 70-year rainfall average for the same months in the Gainesville area (McCloud, 1979). The high rainfall in July and August, poor soil drainage, and high temperatures caused stunted plants and shortened the growth cycle of the cultivars (Valle, 1978). A high relative humidity also increased leaf, stalk, and ear diseases, which severely decreased yields (Valle, 1978; Chapman et al., 1978).

Vegetative yields were taken throughout the growing season (Fig. 3). Differences in total dry weight between cultivars at day 23 were not statistically significant. However, from day 43 through 78 total dry weights for the hybrid were significantly greater than for the inbred. The stalk dry weight of the hybrid increased to a maximum of

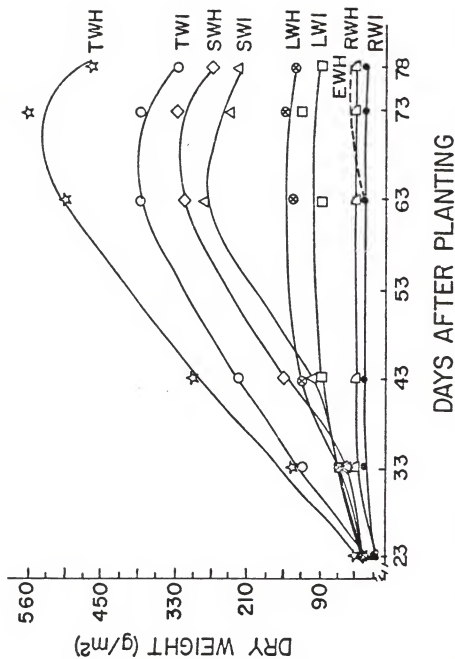


Figure 3. Total, stalk, leaves, roots, and ear dry weight accumulation for the hybrid (H) Pioneer Brand 3369A and the inbred line (I) Iowa 837 studied in 1978.

337.3 g m⁻² at day 73 and then declined. Peak stalk dry weight for the inbred was 279.0 g m⁻² at day 63. Leaf dry weight increased for both cultivars until day 43. Both cultivars maintained a plateau in the leaf weight component from day 43 to 73. Maximum leaf weight at day 73 for the hybrid and inbred were 157.8 and 122.0 g m⁻², respectively. Statistical significances ($p = 0.05$) in the leaf dry weights between the two cultivars were found from day 43 until the end of the experiment.

Pollination occurred at day 53 for the hybrid and 55 for the inbred. Maximum dry ear weight for the hybrid was 30.5 g m⁻² at day 78. From day 63 to 73 (the period of linear ear growth) the hybrid accumulated 34% in the stalks of the total dry weight produced in this period, 52% in the leaves, and 14% in ear growth. There was no reproductive component in the inbred.

Crop Growth and Ear Growth Rates

The rate of dry matter accumulation (CGR) was calculated for both cultivars from day 23 to 63 after planting. The CGR values for hybrid and inbred were 12.2 and 9.1 g m⁻² day⁻¹, respectively. These CGR values were significantly different at the 0.05 level of probability when ranked by Duncan's Multiple Test procedure. Therefore, with the data obtained and the conditions of this experiment, mean CGR values for hybrid and inbred compared at nearly equal LAI were significantly different, indicating differences in net photosynthesis between them. However, in an earlier study with the same cultivars, Valle (1978) was unable to detect a statistically significant difference for the CGR's for the before anthesis period, although significant differences were found after anthesis.

The EGR, the rate at which the ear was filled, was computed for the hybrid from day 63 to 73 and is expressed by the equation:

$$Y = -16.6 + 0.64 X.$$

Brix Readings

Since by day 55 it was apparent that the hybrid and the inbred line would produce abnormally low yields, it was decided to investigate the level of soluble solids accumulated in the stalks. The hypothesis was that photosynthate that could have gone to the ear would accumulate mainly in the stalk. Data presented in Table 2 show that the mean Brix readings per plot for the hybrid and the inbred at day 83 after planting (columns 9 and 10) were higher for the inbred line. The means, compared using a t-test, were significantly different at the 0.05 level of probability. These results tend to indicate that the photosynthate produced by the inbred line, which could have filled the ear, was accumulated in the stalk to a much greater extent than in the hybrid corn; this suggested that the sink capacity of the inbred was lower.

1979 Experiment

Cultivar Characteristics

The cultivars studied during the 1979 growing season were chosen because of their similar characteristics when grown in Florida (Table 3). The similar height of the cultivars facilitated the field layout used, since seeds of the ancient races, Chapalote and Nal-Tel, as well as Maiz Criollo were scarce.

Emergence of all cultivars began approximately one week after planting. Stands in all plots were nearly perfect; however, skips

Table 3. Characteristics of the cultivars studied in the 1979 growing season.[†]

Cultivar	Plant height	Ear height	Leaves	Ears	Tillers	Anthesis [‡]
	----- m -----		---- number/plant ----			
Chapalote	2.8	1.4	12.7	1.8	2.0	66
Coker 77	2.9	1.4	15.4	1.6	0.1	72
Maiz Criollo	2.8	1.6	16.0	1.1	0.1	71
Nal-Tel	2.6	1.4	14.2	1.8	0.3	65

[†] Mean of 30 plants. The measurements were done 125 days after planting.

[‡] Days from planting.

were replanted with seedlings of similar age and size. Anthesis for Chapalote, Coker 77, Maiz Criollo, and Nal-Tel occurred at day 65, 71, 72, and 66, respectively (Table 3). These dates closely agreed with unpublished results for 1978 of Dr. E. S. Horner (Professor of Agronomy, University of Florida). The early maturing Chapalote had an average of two tillers per plant at the end of the growing season as compared with few or none for the other cultivars. The late maturing Coker 77 and Maiz Criollo produced approximately two or three more leaves than the other two cultivars. The cultivars began to show signs of senescence (dead lower leaves) in the period between days 95 and 105 in Chapalote and Nal-Tel, and at day 115 and 125 in Maiz Criollo and Coker 77, respectively. A high LAI in Coker 77 and Maiz Criollo was maintained for longer periods than in Chapalote and Nal-Tel. The LAI of Chapalote was similar to that of Coker 77 during its reproductive phase (Fig. 4). Nal-Tel had the lowest LAI.

Total Dry Weight

Total dry matter accumulation in all cultivars followed a typical sigmoidal curve (Fig. 5). Total dry weights were not statistically different among cultivars for the first 55 days of crop growth. By day 65, Chapalote, Maiz Criollo, and Coker 77 had produced more dry weight than Nal-Tel. However, the dry weight of Coker 77 and Maiz Criollo did not differ statistically from that of Nal-Tel. Total dry weights for Chapalote and Coker 77 at day 75 were significantly greater than those of Maiz Criollo and Nal-Tel due to higher weights of their stalk and leaf components.

From day 85 until the end of the experiment, the total dry weight of Coker 77 significantly differed from the other cultivars. This

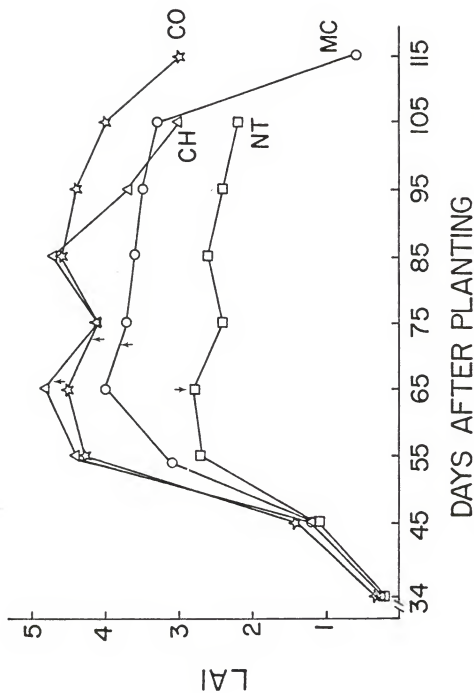


Figure 4. Leaf area index for the maize cultivars grown in 1979. CH = Chapalote; CO = Coker 77; MC = Maiz Criollo; NT = Nal-Tel. Arrows indicate anthesis dates.

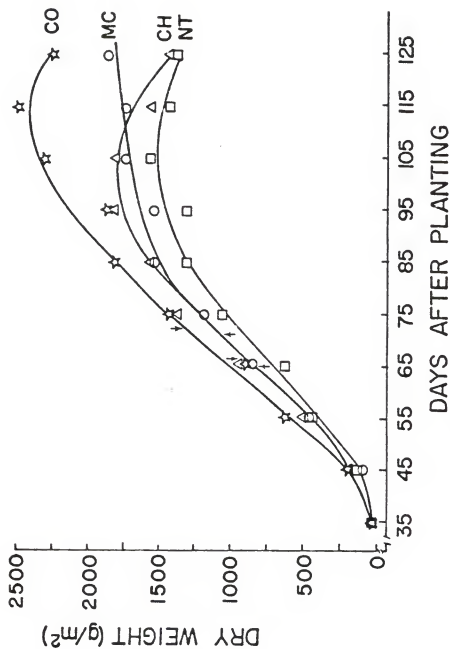


Figure 5. Total dry matter accumulation for the maize cultivars grown in 1979. CH = Chapalote; CO = Coker 77; MC = Maiz Criollo; NT = Nal-Tel. Arrows indicate anthesis dates.

difference was mainly the result of its high ear dry weight. During this period Nal-Tel had consistently lower total dry weights. Chapalote and Maiz Criollo were intermediate.

Peak dry weight for Coker 77 was 2476 g m⁻², recorded at day 115. Chapalote, Maiz Criollo, and Nal-Tel had peak dry weights of 1838, 1848, and 1563 g m⁻², respectively, which were measured at day 95 in Chapalote, day 105 in Nal-Tel, and day 125 in Maiz Criollo. While Chapalote, Coker 77, and Nal-Tel showed decreased total weight at day 125, Maiz Criollo showed increases as a result of ear weight increase.

Root Dry Weight

Root dry weight increased in all cultivars until day 75, after which a plateau was maintained throughout the experimental period. Average root dry weights during the plateau were 123, 193, 163, and 81 g m⁻² for Chapalote, Coker 77, Maiz Criollo, and Nal-Tel, respectively. Mean root weight of Coker 77 was significantly greater than those of Chapalote and Nal-Tel.

Stalk Dry Weight

Dry weight in the stalk (Fig. 6) differed significantly among the four cultivars. Peak stalk weights for Chapalote, Coker 77, Maiz Criollo, and Nal-Tel were 980, 1003, 873, and 855 g m⁻², respectively. After day 85 all cultivars showed a decline in stalk weight, but the degree of decrease varied widely among them. The rate of decline in Chapalote was markedly more pronounced than in the other cultivars. Stalk dry weight in Nal-Tel declined rapidly after day 85 but less rapidly than in Chapalote.

Decreases in stalk weight occurred at the initiation of the ear linear phase which began at day 85 in Coker 77, Maize Criollo, and

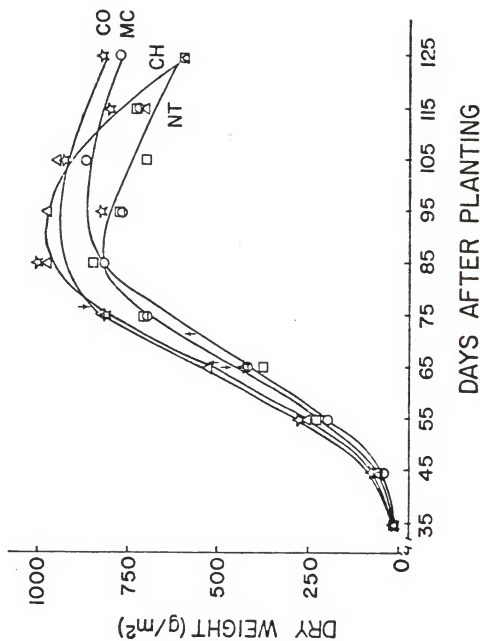


Figure 6. Stalk dry matter accumulation for the maize cultivars grown in 1979. CH = Chapalote; CO = Coker 77; MC = Maiz Criollo; NT = Nal-Tel. Arrows indicate anthesis dates.

Nal-Tel. However, Chapalote increased stalk weight until day 85, but its linear ear growth phase began at day 75. Since Chapalote tillered profusely (up to 12 tillers were counted in several plants before and after anthesis) the increase in stalk dry weight was likely the result of tiller growth. Nal-Tel continued increasing stalk weight from anthesis to the beginning of its linear ear growth. This period was longer than those of the other cultivars. The continued stalk growth into linear ear fill reduced the amount of photosynthate available for ear growth. The decrease in stalk dry weight after day 85 in all cultivars is assumed to be due to translocation of assimilates to the growing kernels.

Leaf Dry Weight

Leaf dry weight in all cultivars increased rapidly until new leaf formation was completed at about day 65 (Fig. 7). After day 65 Coker 77 had the highest leaf weight, whereas Nal-Tel had the lowest; for the latter even the slope of its linear increase leaf weight phase was distinctly different. Peak leaf-weight components were 345, 350, 300, and 217 g m⁻² for Chapalote, Coker 77, Maiz Criollo, and Nal-Tel, respectively. From day 65 the leaf component of Chapalote, Coker 77, and Maiz Criollo formed plateaus for periods varying from 20 to 50 days until leaf senescence started; Coker 77 had the longest and Chapalote the shortest plateau. After reaching its peak weight at day 75, the leaf dry weight of Nal-Tel showed a steady decrease until the end of the experiment. The decline in leaf weight was more pronounced in Chapalote and Maiz Criollo than in Coker 77 or Nal-Tel.

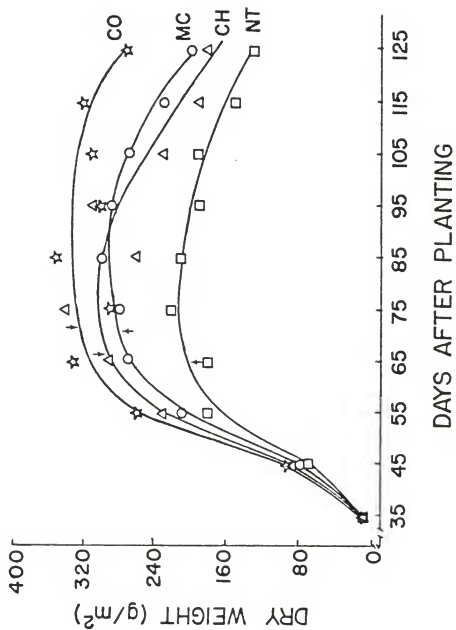


Figure 7. Leaf dry matter accumulation for the maize cultivars grown in 1979. CH = Chapalote; CO = Coker 77; MC = Maiz Criollo; NT = Nal-Tel. Arrows indicate anthesis dates.

Ear Dry Weight

Dry matter in the ear component differed significantly among cultivars (Fig. 8). From day 85 throughout day 125, Coker 77 had a significantly greater ear weight than the other cultivars. The ear weight of Chapalote was the lowest from day 105 until the experiment ended, while Maiz Criollo and Nal-Tel were between the two extremes. Maximum ear weights were 1146, 578, 776, and 607 g m⁻² for Coker 77, Chapalote, Maiz Criollo, and Nal-Tel, respectively. Ear dry weight of Coker 77 at the final harvest was 1023 g m⁻².

Dry Matter Distribution

Root, stalk, leaf, and ear computed as a percentage of the cultivars' total dry weight are presented in Table 4. Root percentages were higher in the vegetative phase. The decrease in root percentage during the reproductive phase was the result of root dry weight plateaus from anthesis, or shortly after, until the end of the experiment, while the total dry weight of the cultivars continued to increase. From day 65 to day 125 the percentage of total dry matter comprising the stalk component was lower in Coker 77 and Maiz Criollo than in Nal-Tel or Chapalote. The stalk component percentage of Coker 77 was the lowest. Stalk component percentages of Chapalote and Nal-Tel were higher than that of Coker 77 and Maiz Criollo due to continued growth of tillers in Chapalote and stalk weight increase in Nal-Tel between day 65 and 85.

Coker 77 had higher ear percentages than the other cultivars; Coker 77 had the highest and Chapalote the lowest. From day 85 to 115 Maiz Criollo had the highest leaf component percentage ranging from 13.3 to 19.5%; it was also the variety with more leaves (Table 3).

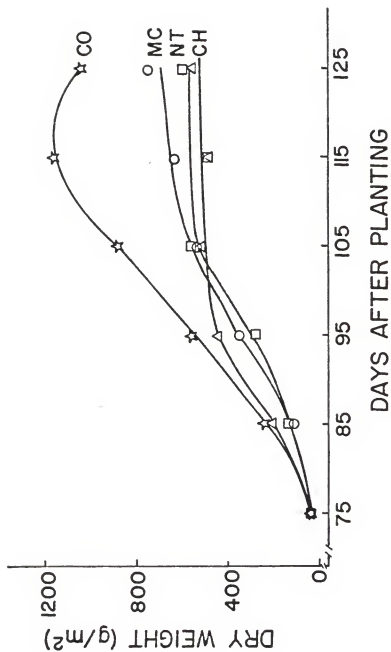


Figure 8. Ear dry matter accumulation for the maize cultivars grown in 1979. CH = Chapalote; CO = Coker 77; MC = Maiz Criollo; NT = Nal-Tel.

Table 4. Dry matter distribution as percent of the total dry weight of the maize cultivars grown in 1979.

Days after planting	Plant Components																	
	Roots			Stalks			Leaves						Ear					
	CH†	CO	MC	NT	CH	CO	MC	NT	CH	CO	MC	NT	CH	CO	MC	NT		
	----- % -----																	
34	17.0	14.6	13.0	15.1	33.0	33.3	32.0	33.3	50.0	52.1	55.0	51.6						
45	11.6	10.0	11.5	9.4	36.2	40.2	36.3	42.0	52.2	49.8	52.2	48.6						
55	10.5	11.2	14.3	10.1	45.1	46.5	42.2	49.4	44.4	42.3	43.5	40.5						
65‡	11.6	13.7	19.2	12.6	56.9	49.1	49.5	59.0	31.5	37.2	31.3	28.4						
75§	10.3	18.0	15.0	10.8	61.1	58.4	59.1	65.3	25.3	20.5	24.0	19.9	3.3	3.1	1.9	4.0		
85	8.5	12.6	18.0	6.6	62.6	54.8	54.3	66.6	16.5	19.1	19.5	16.2	12.4	13.5	8.2	10.6		
95	6.3	8.3	8.5	5.2	53.3	45.2	49.8	59.0	17.0	16.3	18.4	14.2	23.4	30.2	23.3	21.6		
105	6.0	7.6	5.8	5.8	52.6	40.0	49.4	45.4	12.8	13.6	15.3	12.3	28.6	38.8	29.5	36.5		
115	10.8	8.5	10.5	5.0	45.0	32.4	40.6	49.7	12.3	12.8	13.3	10.3	31.9	46.3	35.6	35.0		
125	5.2	6.0	5.4	4.0	42.2	36.3	41.8	43.5	12.5	12.1	10.8	9.2	40.1	45.6	42.0	43.3		

† CH = Chapalote; CO = Coker 77; MC = Maiz Criollo; NT = Nal-Tel.

‡ Anthesis date for Chapalote and Nal-Tel.

§ Anthesis date for Coker 77 and Maiz Criollo.

Although Chapalote and Nal-Tel tasseled at day 66 and 65, respectively, the high vegetative component weight up to or well into the ear linear phase is evidence that these cultivars continued distributing photosynthate to vegetative growth. Stalk and leaf component percentages were higher in both cultivars at day 75 and 85 than for Coker 77 and Maiz Criollo. Coker 77 and Maiz Criollo, in spite of their later anthesis at day 72 and 71, respectively, invested a lower fraction of their assimilates into their stalk and leaf components before and after anthesis, and began linear increase in ear weight sooner than the ancient races. In other words, Coker 77 and Maiz Criollo set kernel number and began to fill them with less apportioning of photosynthate to vegetative growth.

Crop Growth Rate

The early exponential phase of the total dry matter sigmoidal curve covered the first 45 days of crop growth (Fig. 5). The cultivars increased dry weight at a linear rate from approximately day 45 to day 85. Vegetative crop growth rates (CGRv) were calculated from day 45 to day 65 in Chapalote and Nal-Tel, and from 45 to 75 for Coker 77 and Maiz Criollo. These periods correspond to beginning of linear total weight increase to anthesis.

Crop growth rates during the vegetative phase for Chapalote, Coker 77, Maiz Criollo, and Nal-Tel are presented in Table 5. These values are the slopes of the respective linear regression equations. Coefficients of determination for each equation were greater than 0.986. The difference in CGRv between Nal-Tel and the other three cultivars is attributed to the lower LAI of Nal-Tel (Fig. 4). It has been shown that the rate of dry matter production in corn increases

105

with increasing LAI and percent light interception (Hanway, 1962; Ragland et al., 1965; Williams et al., 1965a, 1968). Chapalote, Coker 77, and Maiz Criollo had comparable LAI values during most of the experimental period.

Since the CGRv values for Chapalote, Coker 77, and Maiz Criollo were not statistically different, presumably, they also had very similar canopy photosynthesis and potential to produce high yields. Crop growth rate measured from the beginning of the linear phase prior to ear development reflects the rate of net photosynthesis, and hence, assimilate production rate that could be available for ear growth. This assumes, however, that the photosynthate produced would be used exclusively to fill grain, that the rate does not change during grain filling, and the sink capacity is adequate to utilize it.

From the beginning of linear increase in ear weights the rates of total dry matter accumulation decreased for all cultivars. Crop growth rates during linear ear growth (CGRr) for Chapalote, Coker 77, Maiz Criollo, and Nal-Tel are presented in Table 5. Coefficients of determination for the linear regression equations explained more than 90% of the variability in the sum of squares for total dry matter. The CGRr values for Chapalote and Coker 77 were not statistically different from each other, but were significantly different from the CGRr of Maiz Criollo and Nal-Tel.

The decrease in total biomass growth rate during the reproductive period could have been caused by a decrease in photosynthesis with decrease in solar radiation, light interception, leaf aging, or because more photosynthate was required in the production of dry matter in the seed than in the vegetative portion. This last reason, although

Table 5. Crop growth rates, EGR, and distribution index for the maize cultivars grown in 1979.

Cultivars	Days	CGRv†	Div‡	Days	CGRr†	DIR‡	Days	EGR
		g m ⁻² day ⁻¹			g m ⁻² day ⁻¹			g m ⁻² day ⁻¹
Chapalote	45-65	37.6 a*	0.51 b	75-95	23.7 a	0.81 c	75-95	19.2 b
Coker 77	45-75	39.5 a	0.77 ab	85-115	24.0 a	1.27 b	85-115	30.4 a
Maiz Criollo	45-75	34.3 a	0.57 b	85-105	11.3 c	1.74 a	85-105	19.7 b
Nal-Tel	45-65	24.7 b	0.88 a	85-105	13.9 bc	1.56 ab	85-105	21.7 b

† CGRv and CGRr are the CGR measured from the beginning of the linear phase to anthesis and during the linear ear growth rate, respectively.

‡ Div and DIR are the ratios of EGR divided by CGRv and CGRr, respectively.

* Values within columns with the same letter are not significantly different at 0.05% level of probability according to Duncan's multiple range procedure.

important, may not have been the cause of the decrease in total biomass growth rate, since the vegetative portion of a corn plant has a chemical composition similar to the seed (Morrison, 1947; Sinclair and de Wit, 1975). The energy required to produce a unit of seed weight or a unit of vegetative component per gram of photosynthate is nearly equal. These relationships are presented in Table 6.

Production value (Penning de Vries et al., 1974) is defined as the weight of the end product divided by the weight of the substrate required for its formation. The production value can be used to determine the amount of glucose required for synthesis of plant components provided that the chemical composition is known. For example, one gram of maize vegetative matter requires 1.09 grams of glucose while one gram of seed and one gram of cob require 1.29 and 1.05 grams of glucose, respectively. Using a shelling percentage of 83, the ear yield component of the plant requires 1.25 grams of glucose. The ratio of the glucose required for the yield component to the vegetative component is 1.15. The 15% increase in photosynthate required to produce the ear component accounts for only a small part of the decrease in total biomass production in the reproductive phase.

A decrease in solar radiation was an improbable cause for the decrease in total biomass growth rate during reproductive growth, since the average daily irradiance during reproductive growth, June and July, was the highest of the experimental period (McCloud, 1980). Leaf area index maintained plateaus during most of the vegetative and reproductive growth (Fig. 4). Thus, light interception can be assumed the same in both periods.

Table 6. Estimation of glucose required for synthesis for the vegetative, seed, and cob components of a maize plant.

Component	%	PV †	Glucose required for synthesis
		g g ⁻¹	g g ⁻¹
Vegetative ‡			
Carbohydrate	80	0.853	0.938
Protein	6	0.620	0.097
Lipids	2	0.351	0.057
Grain §			
Carbohydrate	84	0.853	0.985
Protein	10	0.620	0.161
Lipids	5	0.351	0.142
Cobs ‡			
Carbohydrate	86	0.853	1.008
Protein	2	0.620	0.032
Lipids	0.4	0.351	0.011

† Production Value (Penning de Vries et al., 1974)

‡ Chemical composition from Morrison (1947)

§ Chemical composition from Sinclair and de Wit (1975).

Most of the decrease in crop growth during ear development (CGRr) may have resulted from a decrease in apparent photosynthesis or CER (Shibles, 1976) as Vietor et al. (1977), Crosbie et al. (1977), and Wilhelm and Nelson (1978b) have shown. These studies showed decreases in photosynthetic rates with leaf aging sufficient to account for the decrease in growth rate (CGRr) during the reproductive phase measured in this experiment. There was also rain deficit during the grain filling period. Irrigation as supplied may not have been as uniform as expected; dry soil caused wilting and hence reduction in photosynthesis.

It should be recalled that the increase in dry weight in Chapalote during the vegetative, and part of the reproductive growth phases, was the result of main stalk growth as well as growth of tillers most of which were barren. Thus, CGRv as a measurement of dry matter increase for crop growth that could be available for ear growth would be applicable only to varieties which allocate photosynthate more completely to ears. The high CGRv of Chapalote was a composite of potentially available photosynthate for ear growth and photosynthate invested into tiller growth. The CGRr of Chapalote thus decreased either because photosynthesis decreased as leaves aged or it may have decreased because of lack of sink.

The change in growth rate for the period after anthesis and during linear ear growth may be exemplified better in Maiz Criollo. This is a cultivar that did not tiller and had a high CGRv not statistically different from that of Chapalote or Coker 77. However, its total dry matter accumulation rate changed drastically during the period of reproductive growth. This reduction in growth rate, as stated above,

likely could have resulted from a decreased canopy photosynthesis which assimilate production had to be diverted into two sinks, i.e., ear growth and stalk growth, as did Chapalote. However, the decrease in dry weight for the leaf and stalk components after day 95 and 105, respectively, suggests remobilization and translocation of assimilates for ear growth (Figs. 6 and 7).

These considerations are also applicable to Coker 77 and Nal-Tel; although these cultivars did not continue increasing stalk weight after the beginning of linear ear growth. Coker 77 had almost double CGRr which was maintained for a longer period and also less translocation of assimilates to the ear than the other cultivars, as is evident by its lower decrease in stalk and leaf dry weights during the reproductive period.

Ear Growth Rate

The cultivars began to increase ear dry weight at a linear rate around day 75 for Chapalote and day 85 for the other cultivars (Fig. 8). Ear growth rates were computed using linear regression analysis (Steel and Torrie, 1960). These rates are presented in Table 5. The EGR of Coker 77 was significantly greater than the EGR of Chapalote, Nal-Tel, and Maiz Criollo, while the latter three did not differ significantly from each other.

The EGR is the rate at which the ear is filled. The CGRv, calculated prior to ear development, is taken as an estimation of the rate of potentially available photosynthate for ear development. The quotient of EGR by CGRv is an estimate of the crop's relative increase in ear weight as compared to weight increases in the vegetative fraction, i.e., an estimation of distribution of dry matter for ear

growth. These distribution indices (D_{IV}) for Chapalote, Coker 77, Maiz Criollo, and Nal-Tel were 0.51, 0.77, 0.57, and 0.88, respectively. This means, for example, that Chapalote produced 51% as much as it could have produced had all photosynthate been available at the same rate during seed filling as it was during vegetative growth and 100% of it were allocated to seeds, assuming that grain growth requires equal photosynthetic energy of vegetative growth.

The distribution index in the reproductive phase (D_{IR}), calculated by the ratio of EGR to CGR, is presented in Table 5. Ratios greater than 1.0 resulted because of the decrease in growth rate during the reproductive phase, probably caused by decline in canopy photosynthesis as leaves aged. The D_{IR} ratios may also be interpreted as an indication of translocation to the ear of assimilates, previously stored in vegetative parts, when the demands of the ear became greater than the photosynthate produced. This translocation maintained the ear growth rate constant for most of the filling period.

Ear Effective Filling Period

The presumed linear period over which the ear increases in dry weight until it reaches mature weight is referred to as the effective ear filling period (EEFP). It was calculated by dividing the final yield by the EGR (Table 7), and hence, is a relative measurement of the length of the ear filling period.

Several studies have shown that lengthening the life of a crop increased productivity (Alberda, 1962; Daynard et al., 1971; Van Dobben, 1962). However, the filling period is the period in which assimilate is distributed into the yield component of the plant. Thus, to increase yield, this is the period that should be lengthened.

Table 7. Summary of related yield parameters of the maize cultivars grown in 1979.

	Cultivars		
	Chapalote	Coker 77	Maíz Criollo
Final ear yield (g m ⁻²)	578.0 c*	1023.0 a	776.0 b
EGR (g m ⁻² day ⁻¹)	19.2 b	30.4 a	19.7 b
EEFP (days)	30.1 b	33.7 ab	39.4 a
Shelling percentage (%) †	84.2 ab	81.5 b	81.3 b
AKW ‡ (mg kernel ⁻¹)	183.6 c	297.5 a	266.3 b
KGR (mg kernel ⁻¹ day ⁻¹)	5.0 c	8.5 a	7.5 b
ESFP (days)	36.7 a	35.0 ab	35.5 ab
Kernel number (kernels m ⁻²)	2650.0 a	2802.0 a	2370.0 b
			2474.0 b

* Means within each row followed by the same letter do not differ significantly at the 0.05 level of probability according to Duncan's multiple range test.

† Shelling percentage at the final harvest date. It was obtained from the 5-plant sub-sample.

‡ Average-kernel weight at the final harvest date. It was obtained from 100-kernel weights.

Duncan et al. (1978) found that differences in the EFP, among several peanut varieties and one soybean cultivar, accounted for from 7 to 37% of the yield difference among cultivars. Gay et al. (1980) concluded that a significant portion of the yield difference between an old, low-yielding soybean cultivar and a new high-yielding cultivar was due to an increase in the filling period.

The EEFPs for Chapalote, Coker 77, Maiz Criollo, and Nal-Tel are presented in Table 7. The difference in EEFP between Coker 77 and Chapalote explained 17% of their yield difference. The EEFP also explained 30% of the difference in yield between Coker 77 and Nal-Tel. However, the greater EGR of Coker 77 explained most of the yield differences.

Kernel Growth Components

The weight of 100 kernels, taken at each harvest during the reproductive period, allowed the development of a curve of dry matter accumulation for individual seeds (Fig. 9). The mean rate of dry matter increase in single kernels (KGR) was calculated during linear kernel growth using regression analysis. Single kernel growth rate is genetically controlled, with short-term environmental conditions having minimal effects on the growth rate (Osafo and Milbourn, 1975; Poneleit and Egli, 1979; Tollenar, 1976; Duncan et al., 1965), and as a result of remobilization of assimilates it is relatively independent of current photosynthate supply (Duncan et al., 1965; Poneleit and Egli, 1979).

Significant differences were found among cultivars in KGR (Table 7). Coker 77 had the highest KGR, and Chapalote the lowest.

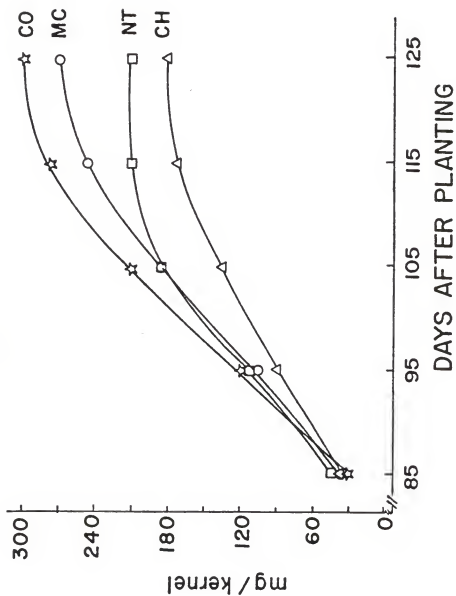


Figure 9. Kernel dry matter accumulation for the maize cultivars grown in 1979. CH = Chapalote; CO = Coker 77; MC = Maiz Criollo; NT = Nal-Tel.

Final average kernel weights (AKW) were significantly different among cultivars at the 0.05 level of probability (Table 7). Effective seed filling period (ESFP) was also determined for the cultivars (Table 7). The ESFP is defined as the quotient of average kernel weight and the average rate of dry matter accumulation during the linear phase of grain growth (Hatfield and Ragland, 1967; Daynard et al., 1971). The ESFP is the time it would take for kernel development if development had proceeded at the same rate from pollination to maturity.

The rate of dry weight accumulation in the ear is a direct function of the number of kernels actively growing. The increase in ear weight occurs at an increasing rate as the number of actively growing kernels continues to increase. In corn, the period when actively growing kernels are added is short, i.e., no more than 10 days (Duncan et al., 1965). The rapid beginning of ear growth in Chapalote indicated that the number of actively growing kernels increased rapidly, since a sum of linear growth rates by the parts, the kernels, must add to increase in linear growth rate by the whole, the ear. The difference between EEFP and ESFP in Chapalote seems to be in that the kernels grew rapidly at early stages, but after the 95-105 day period the rate of kernel weight increase slowed drastically in such a way that after day 95 total ear dry weight increases were not apparent (Fig. 8). Also, Chapalote had a relatively high kernel number per m^2 , which did not fully compensate for its low yield, probably as a result of lower kernel weight (Table 7). Slow growing kernels which may result in large kernel number (Dreyer, 1980) would not give higher yields per se, since the kernel must also have the capacity to grow large.

Coker 77 had a higher KGR, kernel weight, and kernel number than the other cultivars. This would explain its higher yield.

Total Available Carbohydrates

The percentages of TAC for the different plant components are presented in Table 8. Percent TAC in the stalk decreased linearly in all cultivars during the first 55 days of crop growth. Between day 55 and day 85 percent TAC increased to a plateau which ended at day 105 in Nal-Tel, day 115 in Chapalote and Maiz Criollo, and day 125 in Coker 77. Leaf percent TAC also decreased linearly during the first 55 days of growth. During the rest of the experiment leaf percent TAC increased to a maximum and then decreased at the end of the experiment. Percent TAC in the cob component decreased rapidly in Nal-Tel, and maintained plateaus, from day 85 to 105 in Chapalote and from day 85 to 115 in Coker 77 and Maiz Criollo. The percent TAC in the grain was higher in Maiz Criollo and Coker 77 than in the ancient races. Coker 77, the best yielding variety, maintained greater percentage TAC in vegetative components (leaf, stalk, and cob) during reproductive growth than the other varieties; this may indicate greater photosynthate availability.

Total available carbohydrates (TAC) designates the sum of starch, sucrose, and reducing sugars. The TAC are carbohydrates readily available to the plant as a source of energy. Stalk and leaf TAC weights were calculated by multiplying the fraction TAC (Table 8) by the stalk and leaf weights. The cob TAC weight was estimated by multiplying ear yield by shelling percentage; the product was subtracted from ear yield and multiplied by the cob TAC fraction; TAC weight for the grain was

Table 8. Percentages of total available carbohydrates (TAC) for stalks, leaves, cobs, and grain of the maize cultivars studied in 1979.

Days after planting	Stalks †			Leaves			Cobs			Grain		
	CH ‡	CO	MC	NT	CH	CO	MC	NT	CH	CO	MC	NT
	----- % -----											
34	13.5 bc	19.0 a	10.8 c	16.0 ab*	7.4 a	10.0 a	7.4 a	9.1 a				
45	7.4 b	11.3 ab	7.5 b	13.0 a	4.1 a	4.3 a	4.6 a	4.8 a				
55	4.0 bc	6.2 a	3.1 c	5.6 ab	1.0 a	1.1 a	1.0 a	1.0 a				
65 §	12.3 a	12.5 a	7.1 a	12.2 a	2.7 b	4.4 a	3.1 ab	3.0 b				
75 ¶	14.7 c	22.5 a	13.8 d	17.2 b	4.4 a	4.6 a	4.4 a	4.2 a				
85	20.7 b	24.8 a	16.1 c	19.0 b	2.8 ab	3.8 a	2.1 b	2.5 ab	13.1 c	20.2 b	29.0 a	16.5 bc
95	19.7 ab	23.0 a	16.8 b	19.4 ab	4.0 b	6.3 a	4.1 b	2.4 b	11.6 b	20.4 a	20.1 a	14.7 ab
105	21.0 abc	24.2 a	18.8 bc	16.0 c	3.2 b	9.1 a	5.4 b	3.3 b	13.1 c	28.4 a	20.5 b	8.6 d
115	16.0 b	25.0 a	15.8 b	9.0 c	2.0 c	7.2 a	4.8 b	0.1 d	6.0 c	20.8 a	17.7 b	4.1 c
125	13.3 b	24.0 a	11.0 bc	8.4 c	1.4 bc	6.7 a	2.6 b	0.7 c	2.0 c	15.4 a	9.6 b	2.2 c
										65.3 ab	68.2 a	62.1 b

* Values with same letter within row and plant component are not statistically different according to Duncan's multiple range procedure.

† Stalks = stem, sheaths, and husks.

‡ CH = Chapalote; CO = Coker 77; MC = Maiz Criollo; NT = Nal-Tel.

§ Anthesis date for Chapalote and Nal-Tel.

¶ Anthesis date for Coker 77 and Maiz Criollo.

obtained by multiplying ear yield by shelling percentage which product was multiplied by the TAC fraction in the grain.

The TAC weights for stalks of Chapalote, Coker 77, and Nal-Tel at day 34 did not differ statistically; however, the stalk TAC of Chapalote was not significantly different from that of Maiz Criollo, which was the lowest.

From day 34 to the end of the experiment, Coker 77 had significantly higher TAC weights in its stalk and leaves than the other cultivars (Figs. 10 and 11). Peak stalk TAC weight in Coker 77 was 250 g m^{-2} at day 85. Coker 77 had one of the slowest remobilization rates of stalk TAC. Leaf TAC increased from 3 g m^{-2} , at day 34, to a maximum of 30 g m^{-2} at day 105, decreasing to 18 g m^{-2} at the final harvest.

Peaks of stalk and leaf TAC for Maiz Criollo were 164 and 15 g m^{-2} , respectively, at day 105, decreasing to 85 and 5 g m^{-2} at day 125.

Stalk TAC of Chapalote and Nal-Tel peaked at 207 and 163 g m^{-2} , at day 105 and 85, respectively. Leaf TAC, in both races, peaked at day 75 with weights of 15 and 9 g m^{-2} , respectively.

Total available carbohydrates in the cob component of Coker 77 and Maiz Criollo were significantly higher than in Chapalote and Nal-Tel from day 85 throughout the end of the experiment (Fig. 12). The cob TAC of Coker 77 was almost double that of Maiz Criollo. Peak TAC weights for the cob of Chapalote, Coker 77, Maiz Criollo, and Nal-Tel were 15 , 56 , 26 , and 10 g m^{-2} , respectively. Peak weights were recorded at day 85 for Nal-Tel, day 95 for Chapalote and Maiz Criollo, and day 105 for Coker 77. From peak dates, TAC in the cob decreased until the end of the experiment.

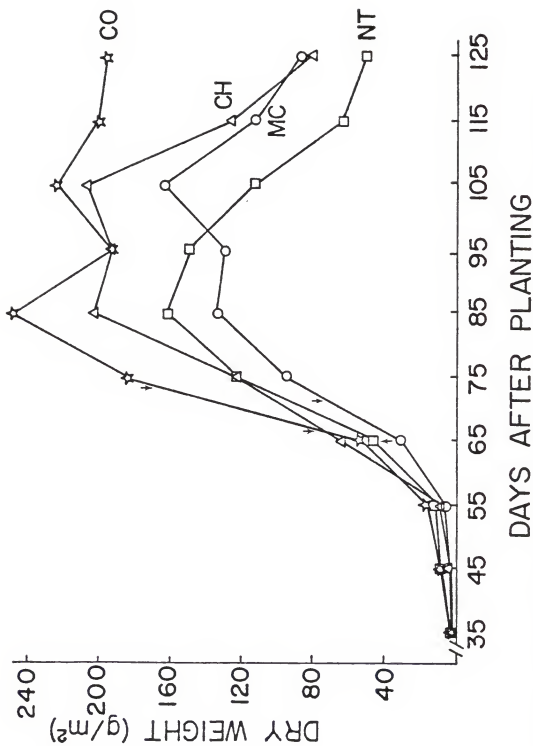


Figure 10. Stalk TAC weight in the maize cultivars grown in 1979. CH = Chapalote; CO = Coker 77; MC = Maiz Criollo; NT = Nal-Tel. Arrows indicate anthesis dates.

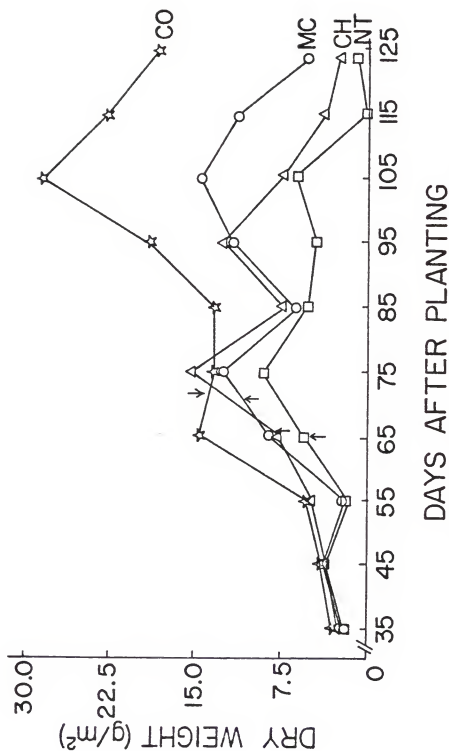


Figure 11. Leaf TAC weight in the maize cultivars grown in 1979. CH = Chapalote; CO = Coker 77; MC = Maiz Criollo; NT = Nal-Tel. Arrows indicate anthesis dates.

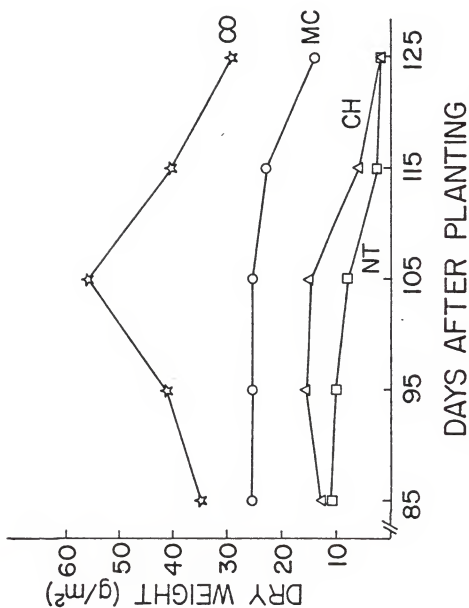


Figure 12. Cob TAC weight in the maize cultivars grown in 1979. CH = Chapalote; C0 = Coker 77; MC = Maiz Criollo; NT = Na1-Tel.

Total available carbohydrates in the grain increased rapidly in all cultivars. Grain TAC in Coker 77 was significantly higher than grain TAC of the other cultivars; Coker 77 was followed by Maiz Criollo and finally Nal-Tal and Chapalote (Fig. 13).

From the beginning of grain TAC increase, at day 85, until maximum grain TAC weight was reached, at day 115 in Coker 77 and day 125 in Chapalote, Maiz Criollo, and Nal-Tel, they gained 649, 243, 409, and 277 grams TAC per m^2 , respectively. Assuming that the decrease in TAC in the other components (from their maximum to their minimum weight) is translocated to the grain, it would explain 9, 26, 13, and 21% of the final yield of the cultivars in the same order. Coker 77 and Maiz Criollo had more TAC in leaf and cob than Chapalote and Nal-Tel. Apparently high cob TAC may be indicative of a good driving mechanism.

The assumption that the summation of the decrease in TAC weight in the different components is translocated to the ear has to be viewed with caution, since it is possible that a fair amount of that TAC could have been respired. However, it is worth noting that the decrease of TAC in the leaf component of Coker 77 was much lower than in the other cultivars. Also, its stalk TAC declined quite slowly. This could have resulted from greater photosynthate production.

The decrease in TAC in the various plant components, assumed to indicate carbohydrate translocation to the grain during the reproductive phase, was greater as canopy senescence progressed. As mentioned before, canopy senescence began at day 95 and 105 in the ancient races, day 115 in Maiz Criollo, and was appreciable only at day 125 in Coker 77.

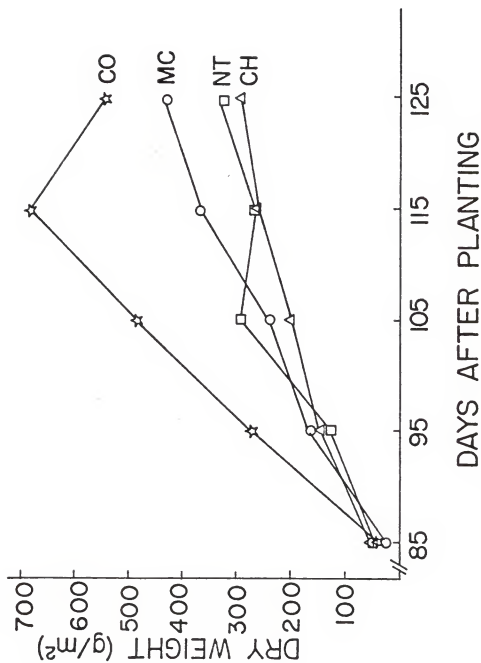


Figure 13. Grain TAC weight in the maize cultivars grown in the 1979 growing season. CH = Chapalote; CO = Coker 77; MC = Maiz Criollo; NT = Nal-Tel.

Brix Readings

Percent Brix readings in corn cultivars, measured either in sap from the whole stalk or internode by internode, could be used as an indication of inadequate sink capacity or inadequate photosynthesis. It is reasonable to assume that photosynthate that is not translocated to the ear should accumulate, mainly in the stalk and then in leaves and roots. Also, if photosynthate is decreasing due to stress, the ear could withdraw assimilates from reserves to fill its kernels. The main storage of assimilates are the lower internodes, because they have greater capacity than the top internodes thus containing more of the sap in which soluble solids are stored, and because photosynthate produced by leaves in the top internodes is rapidly utilized by the growing ears. Thus, it would be in the lower internodes that a change in Brix should reflect accumulation or withdrawal of assimilates more accurately.

Refractometric readings per plot in the four cultivars studied are shown in Fig. 14. The influence of high Brix in the top internodes of Coker 77 could be the cause for the higher Brix readings per plot during the last part of its growth cycle. However, its lower internodes (2nd, 4th, and 6th), as well as the lower internodes of the other three cultivars, increased by more than 100% from the vegetative to the reproductive phase.

Average percent Brix readings (APBR) in the different internodes are presented in Figs. 15, 16, 17, and 18. The figures show only the APBR until the 10th internode. Chapalote's APBR increased rapidly until day 85, from which the 6th, 8th, and upper internodes maintained plateaus until day 105. The 2nd and 4th internodes continued increasing

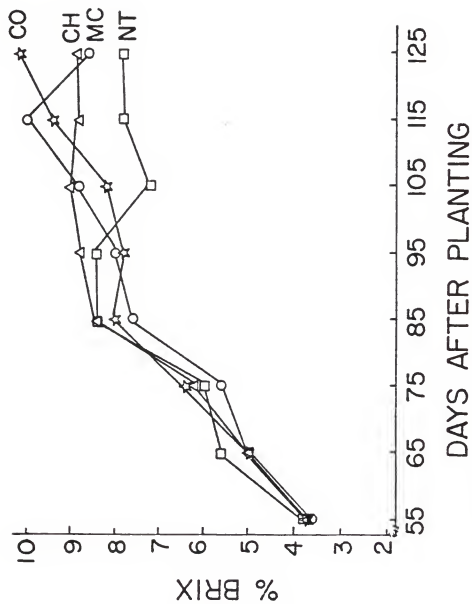


Figure 14. Average percent Brix readings per plot in the cultivars grown in 1979. CH = Chapalote; CO = Coker 77; MC = Maiz Criollo; NT = Nal-Tel.

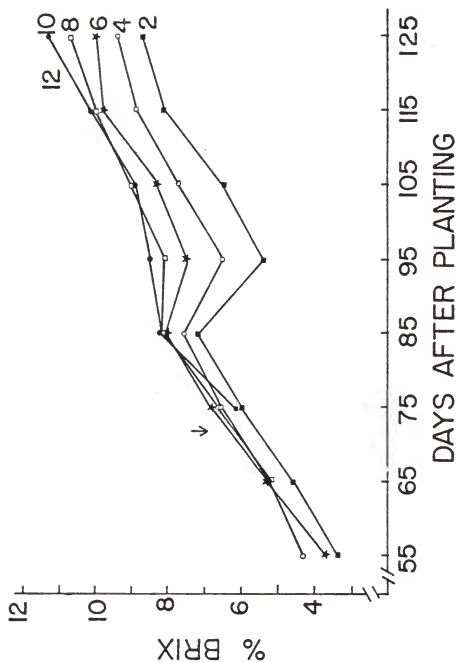


Figure 15. Average percent Brix readings per internode in Coker 77. Smaller numbers indicate lower internodes. Arrow marks anthesis date.

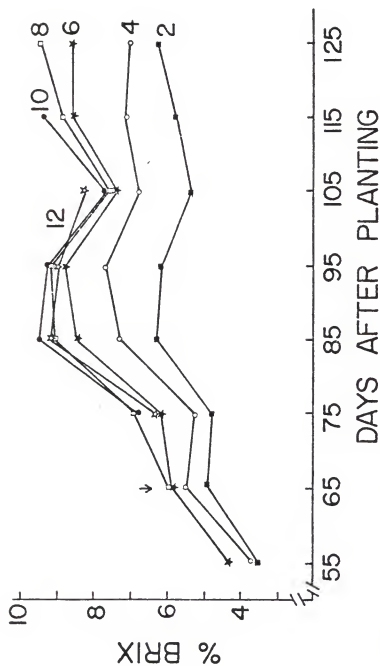


Figure 16. Average percent Brix readings per internode in NaI-Tel. Smaller numbers indicate lower internodes. Arrow marks anthesis date.

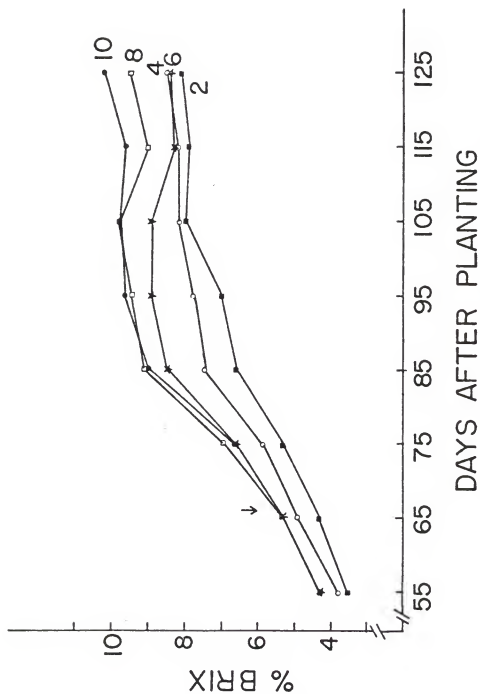


Figure 17. Average percent Brix readings per internode in Chapalote. Smaller numbers indicate lower internodes. Arrow marks anthesis date.

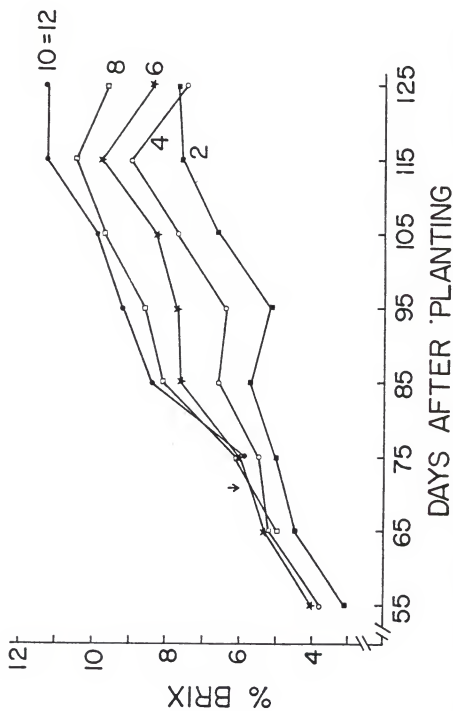


Figure 18. Average percent Brix readings per internode in Maiz Criollo. Smaller numbers indicate lower internodes. Arrow marks anthesis date.

APBR from day 85 throughout day 125 but at a slower rate. In Chapalote as well as in Nal-Tel, the 6th and 8th internodes were usually the internodes bearing ears. Nal-Tel APBR in internodes 2, 4, and 6 increased until day 95, but decreased markedly at day 105. Average percent Brix readings for the 6th, 8th, and 10th internodes were very similar at day 105 and 115.

Internode APBR patterns for Coker 77 and Maiz Criollo were similar. APBR increased in a linear manner in Coker 77 until day 85. From day 85 to 95 the APBR of the 2nd, 4th, and 6th internodes decreased sharply and leveled-off in the 8th. From day 95 until the end of the experiment all the internodes of Coker 77 increased APBR. The ears of Coker 77 and usually one ear in Maiz Criollo were located generally in the 8th and/or 10th internode. The difference between the pattern of Maiz Criollo and that of Coker 77 was that the rate of APBR increase in Maiz Criollo until day 105 was slower. Also, the decrease in APBR at day 95, mainly in the lower internodes, was not as pronounced as in Coker 77.

The lower values of the APBR of the lower internodes of Coker 77 during part of its linear ear growth phase were not statistically different from those of Maiz Criollo, Chapalote, or Nal-Tel. However, they may indicate that Coker 77 had a greater sink capacity, which not only used photosynthate produced by the canopy, but also utilized photosynthate stored in those internodes.

Partitioning Coefficient

The partitioning coefficient, or partitioning factor (Duncan et al., 1978), is defined as the division of recent assimilates between reproductive growth as opposed to vegetative growth. In a determinant

crop, particular attention is given to the partitioning that occurs just as the final fruit number per plant is determined. This is because, before the final seed number is determined, there are not enough seeds to utilize all the assimilates potentially available for kernel growth. Thus, the plant may continue to grow vegetatively, i.e., produce tillers, or store the assimilates. After final kernel number has been determined, actively growing kernels develop priority for photosynthates, i.e., a polarization of assimilates to the growing kernel established in the early phases of embryo development (Loomis, 1945); however, actively growing kernels may utilize more assimilate than is produced by redistribution or translocation of photosynthates from reserves as the season advances or weather conditions are temporarily unfavorable.

The partitioning coefficient (PC) for the cultivars was calculated by the equation $PC = (Y.KGR) / (CGRv.AKW)$ (Duncan et al., 1980). In this equation Y represents the final yield, KGR is the rate of dry matter increase in individual kernels corrected for energy content and energy of formation, CGRv is the rate of total dry matter accumulation during the vegetative period also corrected for energy content and energy of formation. The CGRv is a measurement of dry matter productivity, and in the context of the formula it is equated as an estimation of net photosynthesis during the period in which kernel number was set; AKW is the average kernel weight equated as a measurement of the average final capacity of individual kernels to accommodate dry matter, i.e., average kernel size (Table 7).

The PCs of Chapalote, Coker 77, Maiz Criollo, and Nal-Tel were 0.45, 0.87, 0.75, and 0.99, respectively. This factor is interpreted as an estimate of the fraction of photosynthate partitioned to kernel

growth, as opposed to vegetative growth or storage at the period in which potential maximum kernel was set. In fact, PC is important at this moment since it would determine the number of kernels that may develop into final yield, provided that climatic and nutritional conditions are favorable.

The lower PC of Chapalote is in agreement with earlier considerations about distribution of photosynthate between main stalk growth and tiller growth. Chapalote was still growing tillers in the middle of its linear ear growth phase, presumably, partitioned less of its assimilates to ear development.

The PC is limited by factors other than photosynthate supply, since increases in TAC in vegetative components occurred before and after anthesis. In other words, cultivars like Chapalote, Maiz Criollo, and Nal-Tel, probably had to satisfy the needs of two sinks, the reproductive and the vegetative sinks. Thus, the PC limiting kernel number also acted to satisfy vegetative needs. However, once vegetative needs were satisfied translocation of assimilates from vegetative components occurred due to leaf senescence and decrease in leaf photosynthesis, and because one of the components of sink capacity, final kernel size, was yet to be satisfied. However, in the period of kernel number adjustment, basal kernels may begin to grow sooner than kernels at the tip of the ear, simply, because they are receiving photosynthate more directly. Thus, an explanation for the lower weight of tip kernels may be their shorter filling periods. This may be caused by a late beginning of their linear growth rates and an earlier cessation of development, probably due to atrophy of vascular bundles as basal kernels stop growing.

Yield Dynamics

The four cultivars differed significantly in final ear dry weight. The ancient races had the lowest yield. The yield of Maiz Criollo was 34% and 28% higher than that of Chapalote and Nal-Tel, respectively. The hybrid, Coker 77, yielded 32% more than Maiz Criollo, and almost doubled the yield of the ancient races. The total yield increase of Coker 77 was 59% greater than the average yield of the three cultivars and 73% greater than the average yield of Chapalote and Nal-Tel.

The capacity for dry matter accumulation of the cultivars as measured by the CGRv did not differ significantly. The statistically lower CGRv of Nal-Tel was caused primarily by its lower LAI. Crop growth rate is a measurement of the integrated metabolic processes that the plant performs for carbon fixation. Among its more important components are the photosynthetic and respiratory rates. In this experiment a direct measurement of these rates was not done. However, the net result of these processes, the CGRv, was not different among Chapalote, Coker 77, and Maiz Criollo. This tends to indicate potential for similar yields.

Corn, a determinant plant, ceases vegetative development at anthesis or shortly thereafter (Hanway, 1971). As the plant changes from the vegetative to the reproductive phase, the PC determines allocation of photosynthate for ear development. Chapalote, with the smaller PC, continued distributing assimilates to tiller growth. The tillers were not only barren and, therefore, represented a diversion of growth potential from the ears, but also shaded main stalks. Shading, to some extent, could have decreased ear dry matter

accumulation by reducing photosynthesis of the main ear-bearing stalk. This may have caused a poor estimate of the CGRv for the main stalk in Chapalote. If the PC could have been computed for the main stalk only, it might have been higher. Nal-Tel continued allocation of photosynthate into the stalk component for a longer period than the other cultivars (anthesis occurred at day 65 and beginning of linear ear growth at day 85), again diverting growth potential from ears. Nal-Tel had a high PC, but also had a lower photosynthetic rate (CGRv) which did not produce enough assimilate for a high yield.

Diversion of growth potential from ears is closely shown in Maiz Criollo which increased TAC in the stalk component well into its linear ear growth phase. This may have resulted because of its lower PC. No explanation for the lower PC of Maiz Criollo is evident in the data obtained.

The rate of total dry matter increase during the reproductive period (CGRr) varied widely among cultivars, and although the CGRr for Chapalote and Coker 77 were similar, the CGRr of Coker 77 was maintained for a longer period. This fact reflects the greater ability of Coker 77 to maintain a higher rate of photosynthesis and higher LAI during seed filling. The decrease in CGRr in the four cultivars is assumed to be caused mainly by a decrease in canopy photosynthesis as the leaves aged. This decrease was more pronounced in the ancient races and Maiz Criollo than in Coker 77.

Filling periods, estimated as EEFP or ESFD, did not provide explanation for the higher yield of Coker 77. The explanation for the higher yield of Coker 77 with respect to Maiz Criollo and Chapalote (the cultivars with CGRr not significantly different from Coker 77)

appeared to be its greater PC that triggered the development of more kernels and thus, a greater sink which better utilized photosynthate produced and/or translocated.

SUMMARY AND CONCLUSIONS

During the 1978 growing season, the hybrid maize Pioneer Brand 3369A and the inbred Iowa B37 were planted (in a completely randomized design with four replications) at populations which provided conditions of nearly equal LAI to allow comparisons. This study showed that soluble solids were accumulated to a higher degree in the stalk component of the inbred line. This suggested that the higher yield of the hybrid was caused by its higher PC.

In 1979 four cultivars were compared in a split-plot arrangement with four replications. The cultivars were: two ancient races, Chapalote and Nal-Tel; a Cuban accession, Maiz Criollo; and a high yielding hybrid developed in the south-east USA, Coker 77. Growth analysis indicated that the rate of dry matter production in the vegetative phase (CGRv) for Chapalote, Coker 77, and Maiz Criollo were not statistically different. The difference of CGRv between Nal-Tel and the other cultivars was probably the result of its lower LAI.

The similar CGRv of Chapalote, Coker 77, and Maiz Criollo suggested a similar potential for higher yields. However, the CGRv of Chapalote included a heavy growth of tillers and thus only the CGRv of the main stalk could be considered potential assimilate for ear growth.

The partitioning coefficient (PC), used as an estimate of the distribution of assimilates for ear growth as opposed to vegetative growth or storage at the period of kernel number set, was higher in

Coker 77 than in Chapalote or Maiz Criollo. Nal-Tel had the highest PC but also the lower photosynthetic rate (lowest CGRv) which was not enough to set a greater sink capacity, thus its low yield.

Coker 77 maintained a higher LAI and total dry matter accumulation rate during reproductive growth (CGRr) than the other cultivars. Also, the hybrid had a greater rate of accumulation of ear weight (EGR) than Chapalote or Maiz Criollo.

It follows that Coker 77 had a better combination of sink capacity in terms of kernel number and size than Chapalote or Maiz Criollo. Chapalote had a relatively high kernel number that did not fully compensate for its lower yield, probably because of its lower kernel size. Total available carbohydrates (TAC) measured in the stalk, leaf, cob, and grain were higher in the hybrid than in the other cultivars. High percentage TAC in cobs of Coker 77 suggested a better driving mechanism. Translocated TAC from vegetative components contributed 9, 26, 13, and 21% to the final ear yield in Coker 77, Chapalote, Maiz Criollo, and Nal-Tel, respectively.

The results of this experiment support the conclusion that under conditions of equal LAI, high PC, which determines greater sink capacity, and a high production of photosynthate during reproductive growth are the physiological parameters that cause high yield.

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APPENDIX A

AMYLOGLUCOSIDASE-INVERTASE PROCEDURE FOR HYDROLYZING
TOTAL AVAILABLE CARBOHYDRATES (STARCH, SUCROSE) TO REDUCING SUGARS

1. Weigh 0.1 g of ground, thoroughly mixed plant material into a 5 ml Erlenmeyer flask.
2. Add 5 ml of distilled water, cap the flasks with marbles and boil for 3 to 5 minutes.
3. To the cooled flask add 5 ml of 0.2 N acetate buffer, and 1 ml of enzyme mix. Place flasks in a 44° C water-bath for 10 to 12 hours.
4. Remove from bath and cool it.
5. Take aliquots (between 0.2 to 0.5 ml) and put into 15 ml test tubes.
6. Add deionized water (between 5.5 and 5.8 ml) and shake.
7. Take aliquots (between 0.2 and 0.5 ml) and put into 15 ml test tubes.
8. Add 1.0 ml of alkaline reagent in each flask, boil for 20 minutes and then cool.
9. Add 1.0 ml of arsenomolybdate reagent in each flask, fill to 10 ml with deionized water and mix well.
10. Read absorbance at 540 nm with a blank solution as zero. Use set of glucose standards prepared with same procedure for calibrating regression line.

Acetate Buffer: Mix 3 parts of 0.2 N acetic acid and 2 parts of 0.2 N sodium acetate. Titrate final buffer solution to pH 4.8 by addition of either solution. Add a few crystals of thymol to prevent growth of microorganisms.

Enzyme mix for 50 ml fresh daily: Add 1.25 g of amyloglucosidase, 1.25 ml invertase, and 3.75 ml of 0.2 N acetate buffer to 45 ml of deionized water.

Alkaline reagent: dissolve 25 g of anhydrous sodium carbonate, 25 g of potassium sodium tartrate, 20 g of sodium bicarbonate, and 200 g of anhydrous sodium sulfate in 700 ml of deionized water and then dilute to one liter. Dissolve 6 g of cupric sulfate in 40 ml of deionized water followed by one drop of concentrated sulfuric acid. Combine the two solutions.

Arsenomolybdate reagent: dissolve 25.0 g of ammonium molybdate tetrahydrate in 450 ml of deionized water, then add 21 ml of concentrated sulfuric acid. In separate solution dissolve 3.0 g of disodium arsenate in 25 ml deionized water. Combine the two solutions.

Calculate TAC in percentage by:

$$\%TAC = \frac{(OD * slope + intercept) * (Dilution factors)}{wt. (mg)} * 100$$

APPENDIX B

TABLES: SOIL FERTILITY ANALYSIS, DRY WEIGHT OF PLANT
COMPONENTS FOR THE 1978 AND 1979 GROWING SEASONS, TOTAL
AVAILABLE CARBOHYDRATES, AND PERCENT BRIX READINGS

Table B-1. The pH, nitrogen, and double-acid extractable nutrients in the soil used in the 1979 experiment.

Soil	pH (H ₂ O)	N	Double-acid extractable nutrients †			
			P	K	Ca	Mg
----- ppm -----						
Jonesville fine sand‡	6.1	21	116	114	385	60

†0.05 N HCl + 0.025 N H₂SO₄ (ratio 1:4).

‡ Loamy, mixed, thermic Arenic Hapludalf.

Table B-2. Dry weights of plant components, and LAI for the hybrid corn Pioneer Brand 3369A and the Inbred Line Iowa B37 investigated in 1978.

Days after planting	Plant Components										Total		LAI	
	Roots		Stalks		Leaves		Ear							
	Hybrid	Inbred	Hybrid	Inbred	Hybrid	Inbred	Hybrid	Inbred	Hybrid	Inbred	Hybrid	Inbred	Hybrid	Inbred
	----- g m ² -----													
23	6	4	10	8	13	11					29	23	0.3	0.3
33	32	18	50	47	60	53					142	118	1.3	1.4
43	32	18	146	112	122	94					300	224	2.2	2.0
63	32	18	320	279	135	88	24	--	--	511	385	1.6	0.6	
73	32	18	337	248	152	124	30	--	--	551	390	0.3	--	--
78	32	18	274	232	133	83	31	--	--	470	333	--	--	--

Table B-3. Dry weight of plant components of the maize cultivars investigated in 1979.

Days after planting	Plant Components															
	Roots				Stalks				Leaves				Ears			
	CH†	CO	MC	NT	CH	CO	MC	NT	CH	CO	MC	NT	CH	CO	MC	NT
	----- g m ² -----															
34	9	8	7	8	19	19	16	18	28	29	29	28	56	56	52	54
45	19	18	18	14	60	74	57	64	86	92	81	74	165	184	156	152
55	55	68	71	46	240	280	208	223	235	255	215	183	530	603	494	452
65‡	106	120	167	81	521	432	431	381	290	328	273	184	917	880	871	646
75§	141	253	176	118	833	822	694	712	345	288	282	217	45	44	22	43
85	133	230	278	85	978	1003	836	855	258	350	300	208	194	247	126	137
95	116	154	133	68	980	836	780	770	312	302	288	186	430	558	365	282
105	108	175	102	90	952	924	873	700	233	314	270	193	517	897	520	570
115	168	210	185	71	700	802	717	708	191	317	235	146	496	1146	630	500
125	75	135	100	56	608	814	772	610	180	271	200	130	578	1023	776	607
													1441	2243	1848	1403

† CH = Chapalote; CO = Coker 77; MC = Maiz Criollo; NT = Nal-Tel.

‡ Anthesis for Chapalote and Nal-Tel at day 65 and 66, respectively.

§ Anthesis for Coker 77 and Maiz Criollo at day 72 and 71, respectively.

Table B-5. Average percentage Brix readings for plot for the maize cultivars grown in the 1979 growing season.

Days after planting	Cultivars			
	Chapalote	Coker 77	Maíz Criollo	Nal-Tel
	----- % -----			
55	3.8 a*	3.8 a	3.6 a	3.8 a
65	4.9 b	5.1 ab	5.0 ab	5.5 a
75	6.2 a	6.3 a	5.6 a	6.0 a
85	8.4 a	7.9 b	7.6 b	8.3 a
95	9.0 a	8.0 b	8.0 b	8.4 ab
105	8.9 a	8.2 ab	8.8 a	7.2 b
115	9.0 ab	9.5 a	10.0 a	7.8 b
125	8.8 ab	10.2 a	8.7 ab	7.8 b

* Means within a row followed by the same letter do not differ significantly at the 0.05 level of probability according to Duncan's multiple range test.

Table B-6. Average percentage Brix readings per internode for the maize cultivars studied in 1979.

Days after planting	Cul- tivars	Internodes							
		2	4	6	8	10	12	14	16
----- % -----									
55	CH	3.5 a*	3.8 a	4.3 a					
	CO	3.4 a	3.7 a	4.3 a					
	MC	3.1 a	3.8 a	4.0 b					
	NT	3.5 a	3.7 a	4.3 a					
65	CH	4.3 a	4.9 a	5.3 a	5.3 a				
	CO	4.6 a	5.3 a	5.3 a	5.2 a				
	MC	4.5 a	5.3 a	5.3 a	5.0 a				
	NT	4.9 a	5.9 a	5.9 a	6.0 a				
75	CH	5.3 bc	5.9 bc	6.6 a	6.9 a	6.6 a	6.1 a	5.7 a	
	CO	6.0 a	6.5 a	6.8 a	6.6 a	6.1 a	5.9 a		
	MC	5.0 bc	5.5 bc	6.0 a	6.1 a	5.9 a	5.6 a	4.8 a	
	NT	4.8 c	5.3 c	6.2 a	6.9 a	6.8 a	6.3 a		
85	CH	6.6 a	7.5 a	8.5 a	9.1 a	9.0 a	9.1 a	9.4 a	
	CO	7.2 a	7.6 a	8.1 a	8.2 a	8.2 a	8.3 a	8.1 a	7.4 a
	MC	5.7 a	6.6 a	7.6 a	8.1 a	8.4 a	8.5 a	8.1 a	7.5 a
	NT	6.3 a	7.3 a	8.5 a	9.1 a	9.5 a	9.2 a	8.7 a	
95	CH	7.0 a	7.8 a	8.9 a	9.5 a	9.6 a	9.7 a	9.4 a	
	CO	5.4 b	6.5 a	7.5 a	8.1 a	8.5 a	9.0 a	8.9 a	9.1 a
	MC	5.2 b	6.4 a	7.7 a	8.6 a	9.2 a	9.5 a	9.2 a	8.1 a
	NT	6.2 ab	7.7 b	8.8 a	9.2 a	9.3 a	9.0 a	8.6 a	

Table B-6 - Continued.

105	CH	8.0 a	8.2 a	8.9 a	9.8 a	9.8 a	9.1 a	9.7 a
	C0	6.5 ab	7.7 a	8.3 a	9.0 a	8.9 a	9.0 a	8.2 a
	MC	6.5 ab	7.7 a	8.3 a	9.7 a	9.9 a	9.8 a	9.5 a
	NT	5.4 b	6.8 a	7.4 a	7.6 a	7.7 a	8.3 a	7.9 a
115	CH	7.9 a	8.2 a	8.3 a	9.0 a	9.6 a	10.9 a	8.0
	C0	8.1 a	8.9 a	9.8 a	10.0 a	10.1 a	10.1 a	
	MC	7.6 a	9.0 a	9.8 a	10.5 a	11.3 a	11.4 a	
	NT	5.8 a	7.2 a	8.6 a	8.9 a	9.4 a	10.8 a	
125	CH	8.1 a	8.5 a	8.4 a	9.5 a	10.2 a	9.8 a	
	C0	8.7 a	9.4 a	10.0 a	10.7 a	11.3 a		
	MC	6.7 a	7.5 a	8.4 a	9.6 a	10.7 a		
	NT	6.3 a	7.1 a	8.6 a	9.5 a	10.8 a		

* Means within an internode-date combination followed by the same letter do not differ significantly at the 0.05 level of probability according to Duncan's multiple range test.

CH = Chapalote; C0 = Coker 77; MC = Maiz Criollo; NT = Nal-Tel.

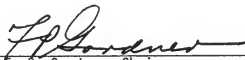
BIOGRAPHICAL SKETCH

Raul Rene Valle Melendez was born 18 March 1951 to Raul Rene and Georgina Melendez de Valle in Tegucigalpa, Honduras.

He attended primary and secondary schools in Honduras finishing in 1968. In 1969 he enrolled at the Universidade Federal de Rio de Janeiro, from which in 1971 he transferred to the Faculdade de Agronomia e Zootecnia "Manoel Carlos Goncalves" in Pinhal, Sao Paulo, Brasil, seeking a specialization in phytology. He received an Engenheiro Agronomo degree in 1972.

After graduation, he worked with the Secretary of Natural Resources in Honduras as assistant and then chief of a seed processing facility. In 1974 he specialized in crop production at the International Center of Tropical Agriculture (CIAT) receiving first place among 25 agronomists of various nationalities. In 1975 he was appointed Sub-Director of an Agricultural Region of Honduras (Region Agricola Centro-Oriental, Danli, El Paraiso), and in 1976 was transferred to Catacamas, Olancho, to work as Director of "Raul Rene Valle" Experimental Sub-Station. In January 1977, he entered the Graduate Program at the University of Florida and received a Master of Science degree in December 1978. He began studies for the Doctor of Philosophy degree at the University of Florida in January 1979. Upon receiving the Ph.D., he expects to return to his country and contribute to its agricultural development. Raul Rene Valle Melendez speaks fluently Portuguese, English, and Spanish (mother tongue). He is a member of the American Society of Agronomy, the Crop Science Society of America, and the Soil Science Society of America.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



F. P. Gardner, Chairman
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March 1981



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